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The Breeding Places of *Phlebotomus* in Panama (Diptera, Psychodidae)[1]

WILFORD J. HANSON

Gorgas Memorial Laboratory, Panama, R. de P.

ABSTRACT

An intensive and prolonged search for the larvae of *Phlebotomus* sand flies in a variety of natural habitats in Panama resulted in the collection of 2258 larvae belonging to at least 15 of the 60-odd species now known from the area. A number of the species are quite specific in their habitat requirements, some living on the surface of fallen dead leaves on the forest floor while others burrow an inch or more beneath the soil surface. Methods used include a sugar solution flotation technique, which is described, and simple searching of likely habitats. The scanty published information is reviewed.

Although *Phlebotomus* sand flies have received much attention because of their transmission of *Leishmania* and other disease organisms, surprisingly little is known of their breeding places. This is true even of the species of the Old World (except perhaps *P. papatasi* (Scop.) and *P. argentipes* Ann. and Brun.), where work with *Phlebotomus* has been carried on for many years.

Perhaps the first *Phlebotomus* larvae ever taken from natural habitats and recognized as such were those found by an assistant of Grassi in a cellar in Rome in 1908. Several adults were reared from these larvae and described by Grassi (1908) as a new species, *P. mascittii*.

Early investigations by Marett (1910, 1913, 1915), Newstead (1911), and Whittingham and Rook (1923) in Malta, Howlett (1913) and Mitter (1919) in India, and King (1913, 1914) in the Sudan, turned up only a few larvae and pupae from natural habitats. Many searches by these workers and others proved fruitless, and the location of breeding places was often merely assumed because of the proximity of resting adults.

It was not until the work of McCombie-Young et al. (1926) in India that substantial numbers of larvae and pupae were found. These workers were the first to apply the flotation technique in the search for *Phlebotomus*, and by this process, in which a saturated solution of sugar was used, they recovered immature stages of *P. papatasi* from soil samples taken in the vicinity of human or animal habitations.

Shortt et al. (1930, 1932) also used this method in finding the breeding places of *P. argentipes* in Assam. They found the larvae of this species to be numerous in and around houses in the top 5 inches of soil rich in organic matter. Smith et al. (1936), while studying the breeding places of *P. argentipes*, found the larvae to be most abundant in loose soil within 20 yards of human or animal dwellings. They also used the flotation technique and recovered, besides *P. argentipes*, immature stages of *P. papatasi* (Scop.), *P. shortti* Adler and Theodor, *P. squamipleuris* Newstead, and *P. babu* Ann., which were then reared to the adult stage.

In other areas, Jerace (1939) in Italy found larvae in debris and soil cracks at or near the base of old walls. Wanson (1942) in Belgian Congo found pupae of *P. freetownensis* Sinton, *P. schwetzi* Adler, Theodor, and Parrot, *P. squamipleuris*, *P. freetownensis niger* Parrot and Schwetz, and *P. wansoni* Parrot in soil near latrines. Nájera (1946) in Spain found larvae in 14 of 130 samples of rubbish taken along streets in Madrid.

In Turkmenistan, Petrishcheva and others (1932, 1935, 1949a, 1949b, 1949c) investigated many possible habitats and obtained immature stages from the following places: land-tortoise nest, mammal burrows, dry excreta of small domesticated animals, dead leaves and rubbish, gerbil nests, and bird nests from holes in dirt banks. Soil samples from these habitats were processed by flotation in a saturated solution of NaCl. In addition, they obtained many adults by placing cages over the entrances of burrows and tree holes and over the ground.

During the course of studies of breeding places by Petrishcheva and Izyumskaya (1941) in Sebastopol, 6 tons of soil were processed, comprising 965 samples, of which 28 contained a total of 61 larvae and 91 pupae. More than 50 percent of the larvae and pupae were taken from floors of houses and animal

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shelters, 32 percent from soil cracks and burrows of rodents, and 18 percent from under stones at the base of walls. None were found in dung heaps, debris under trees, litter from animal shelters, nor in rich soil from gardens.

Nothing was known of the breeding places of New World species until Ferreira et al. (1938) in Brazil reported finding four larvae in material at the base of a tree. Also in Brazil, Lutz (in Castro 1939) obtained adults in cages placed over soil of the forest floor, and Coutinho and Barretto (1941) found one larva of *P. fischeri* Pinto in soil taken at the base of a tree, and from the same material an adult of this species emerged.

Elsewhere, Pifano (1941) in Venezuela found about a dozen larvae in a hole in a wall of a house. Hertig (1942) in Peru examined material from a rock wall which was suspected to be a breeding place because of the presence of white, newly emerged adults. One pupal case was found.

In more recent years, Forattini (1954) in Brazil reared 12 adults of *P. intermedius* Lutz and Neiva from soil samples taken from a pigpen, one more of the same species from soil at the base of a bush and one of *P. pessoai* Coutinho and Barretto from soil at the edge of a stream, both in a forested area. Deane and Deane (1957), also in Brazil, obtained 32 specimens from 241 soil samples, most of which they either processed by flotation in salt solution or kept in the laboratory for emergence of adults. Three species were identified: *P. cortelezzii* Brèthes, *P. longipalpis* Lutz and Neiva, and *P. oswaldoi* Mang. They were taken from the ground in a mule shelter, under rocks, in rock crevices, from the floor of caves, and in scrapings from the trunks of two trees.

Despite the great amount of time and careful work involved, the above investigations in the New World thus turned up little more than 60 specimens, remarkably few considering the effort expended and the abundance of the adults.

The investigations reported here were begun in 1957 by the author and other members of the staff of the Gorgas Memorial Laboratory and were continued until July 1960. During this period an intensive search was carried out for the breeding places of *Phlebotomus*, with especial interest in the six common man-biting species of this area—*P. trapidoi* F. and H., *P. sanguinarius* F. and H., *P. gomezi* Nitz., *P. panamensis* Shan., *P. ylephiletor* F. and H., and *P. pessoana* Barr. Preliminary processing of soil samples by Drs. M. Hertig and P. T. Johnson of the Gorgas Memorial Laboratory, beginning in May 1957, turned up larvae of *Phlebotomus* for the first time in Panama. Since then 370 soil samples have been processed, in addition to numerous direct examinations in the field, yielding 2,258 larvae and pupae, 600 of which have been reared to the adult stage and determined. Samples were taken each month of the year, but mostly during the rainy and early dry season. Several localities on both sides of the Isthmus in or near the Canal Zone, from sea level to about 2000 ft. elevation, were repeatedly visited for obtaining soil samples and searching for immature stages. The places most intensively investigated were: Cerro Galera, on the Pacific side of the Canal Zone; Piña Area, on the Atlantic side near the mouth of the Chagres River; Madden Forest Preserve, nearly midway across the Isthmus in the Canal Zone; and Cerro Campana, in the Republic of Panama about 50 kilometers west of the Canal Zone. Several other areas in the Canal Zone were visited, particularly along abandoned army roads where the forest is relatively undisturbed.

METHODS

The scantiness of information on breeding places of *Phlebotomus* is, no doubt, largely due to the difficulty of isolating the immature stages from the soil. Four methods have previously been used by other workers in finding breeding places: (1) careful direct examination of the soil, debris, etc., (2) placing emergence cages over suspected plots of ground, (3) keeping soil samples in the laboratory within containers, making daily observations for emerging adults, and (4) processing soil by flotation or screening or both. All of these methods require considerable time and patience, but it was found that a combination of flotation using a saturated sugar solution and washing through screens is very satisfactory for ordinary soil samples. It has advantages over methods which involve awaiting the emergence of adults either in the field or laboratory, in that all the larvae and pupae in a given sample are recovered at once. Furthermore, the process itself does not harm the larvae or pupae, which can then be reared to the adult stage and identified. Direct examination is satisfactory for dead leaves and other large objects, but it is very tedious and time-consuming if the sample consists of soil or debris.

The screening-flotation method used in this study is designed to isolate the larvae with as little extraneous material as possible. The samples being processed consist of material which falls into three categories: heavier soil particles which sink and offer no problem; live insects and other members of the soil fauna which sink in water but float in a denser liquid such as saturated sugar solution; lighter material such as bits of leaf, wood and bark, which is present in considerable quantity and complicates the search for larvae. The treatment of the screened fractions with water alone gets rid of this water-floatable material.

The details of the method in practice are as follows: For samples consisting mostly of soil and which do not contain many leaves, twigs or other large objects, (1) the soil is placed in a pan and enough saturated sugar solution added to cover it to a depth of about 2 inches. After considerable agitation by stirring with a tube through which air is bubbled, the sample is left to stand for several minutes. (2) The sugar solution with floating material is then decanted through closely woven Nylon

cloth, from which the collected material is washed into a series of three nested brass gauze sieves, 8 inches in diameter, and with 20, 40, and 60 meshes per inch. With samples containing many leaves or other large floatable objects, the preliminary flotation is omitted and the sample is washed with running water directly into the screens. (3) Most of the larvae are retained by the 40- and 60-mesh screens. These fractions are washed separately into 500 ml. cylinders, which are then filled with water. After allowing a few minutes for any larvae to settle, the water is poured off, thus eliminating the bits of wood, leaves and other water-floatable material. (4) The cylinders are then filled with sugar solution and left for about 10 minutes to allow the living organisms to rise to the surface and the heavier particles to sink. (5) The sugar solution is decanted from the cylinder through a nylon cloth strainer, which, together with the collected sugar-floatable material, is then transferred to a petri dish for examination under the microscope. Enough clean sugar solution is added to the petri dish to allow the living organisms to float. The cloth strainer, a little larger than the petri dish, is crimped radially with four staples so that it lies saucerlike in the petri dish. This is important for rapid microscopic examination, as the gently sloping cloth prevents excessive accumulation around the edge of the surface of the liquid.

The entire washing-flotation process requires at least half an hour, or longer if much organic material is present. Sugar is used instead of salt or other chemicals because it is not toxic to *Phlebotomus* larvae. Most of the larvae are collected on the 40-mesh sieve, the first-instar larvae usually passing on to the 60-mesh sieve. No real attempt has been made to recover eggs. They readily pass through the 60-mesh sieve and only two have been recovered.

LARVAL HABITATS

In table 1 are listed the potential breeding places investigated for immature stages and the number of larvae or pupae recovered.

Table 2 lists by species and habitats those immature forms which were successfully reared to the adult stage and identified. The larval taxonomy has not yet reached the stage which would permit direct identification of the young forms.

Buttresses.—Most of the soil samples, each consisting of about 1 pint to 1 quart of soil, were taken from sheltered areas between tree buttresses, which are outgrowths at the bases of several species of tropical trees. These buttresses may be small and inconspicuous or so large that the space between them equals that of a small room. They often form narrow, deep crevices, or provide a wide variety of other situations, in most cases giving a certain amount of protection from sunlight, rain, and wind. Associated with buttresses are communities of animals similar to those found in hollow trees and rock crevices. Certain species of snails, spiders, scorpions and other arachnoids, crickets, moths, crane flies, mosquitoes, as well as *Phlebotomus* are typical inhabitants, at least during the day. The intensive collecting of adult sand flies by Drs. Fairchild and Hertig since 1943 has shown buttresses to be the richest in species of *Phlebotomus* of all habitats investigated. At least 47 species have been taken there, but the bulk of the specimens were *P. trinidadensis* Newst. and *P. ylephiletor* F. and H., with smaller numbers of *P. shannoni* Dyar. The soil between buttresses often contains considerable organic matter, such as dead leaves, insect fragments, and lizard feces, and would seem to be an ideal habitat for the immature stages of *Phlebotomus*. Therefore, particular attention was devoted to this habitat in the search for breeding places.

A total of 2,123 larvae and pupae, representing at least 11 species, was recovered from this habitat. Most were in the top 2 inches of soil with a few as deep as 4 inches. On two occasions, soil samples

Table 1.—Immature stages of *Phlebotomus* recovered from potential breeding places.

Habitat	Screening-Flotation			Direct Examination
	Samples processed	Samples positive	Larvae or pupae recovered	Larvae or pupae recovered
Between buttresses	245	50	2,123	—
Forest floor, not sheltered (dead leaves)	55	19	39	37
Burrow	27	8	26	—
Hollow tree	12	2	2	—
Under overhanging roots	9	5	16	—
Base of tree	7	3	12	—
Ant-nest refuse	3	1	1	—
Tree hole	3	0	0	—
Bark	2	0	0	—
Under log	2	0	0	—
Under rock	3	0	0	1[a]
Chicken-coop floor	1	0	0	—
Soil cracks	1	0	0	1[a]
Totals	370	88	2,219	39

[a] Pupal case.

Table 2.—Immature stages of *Phlebotomus* from natural breeding places, reared to the adult stage and identified; listed by species and habitat.

Species	Soil between buttresses	Soil from burrows	Soil under roots	Soil at base of tree	Dead leaves, forest floor
panamensis	—	—	—	—	8
pessoana	—	—	—	—	4
trapidoi	1	1	—	—	10
ylephetor	—	—	—	—	2
camposi	—	1	—	—	—
dysponetus	23	—	1	—	—
galindoi	11	—	—	3	1
hamatus	427	5	5	—	—
nordestinus	6	—	—	—	—
ovallesi	24	—	—	—	—
rubidulus	1	—	—	—	—
serranus	35	1	—	—	—
trinidadensis	13	—	—	—	—
vespertilionis	1	—	—	—	—
Species "M"[a]	16	—	—	—	—
Totals	558	8	6	3	25

[a] Now *Phlebotomus hansoni* Fairchild and Hertig. (See Ann. Ent. Soc. America 54(2): 244, 1961.)

from the top inch of soil yielded more than 200 larvae.

The results show little correlation between the numbers of larvae and adults of any given species found in buttresses. Only 13 *P. trinidadensis* larvae have been recovered there, whereas adults of that species sometimes occur in buttresses by the hundreds. It may be that this species burrows to greater depths than those sampled, as it shows a burrowing tendency in laboratory cultures. However, half of the larvae recovered were in the top inch of soil. The immature stages of *P. shannoni,* another common buttress inhabitant in the adult stage, have not been recovered; it shows a surface-feeding tendency in laboratory cultures. *P. hamatus* F. and H., of which only five adults were taken in years of collecting, overwhelmingly dominated the larval population of this habitat. Of the 558 buttress larvae reared and identified, 427 (76.5 percent) were *hamatus.* In certain areas during the rainy season larvae of this species were present in more than half of the samples taken. This species shows burrowing habits in laboratory culture, but it also was found chiefly in the top 2-inch layer. Of the common man-biting species, only one larva of *P. trapidoi* has been taken from this habitat. Two others, apparently either *P. trapidoi* or *P. ylephiletor,* did not survive to yield adults. Both of the latter two species are surface-feeders in laboratory cultures.

Animal burrows.—The 27 samples from animal burrows were taken from 1 to 3 feet inside the entrance; 26 larvae representing at least four species were recovered. One larva of *P. trapidoi,* the only man-biting species taken, was recovered from loose soil and leaf fragments scraped from the floor of a burrow. Again, *P. hamatus* was the dominant species, and of the species of which adults regularly inhabit burrows one larva of *P. camposi* Rodr. was found. It should be noted that the immature stages of *P. triramulus* F. and H., which as adults often occur in burrows in great numbers, have never been recovered.

Hollow trees.—Detritus at the bottom of hollow trees have yielded but two larvae even though adults (*vespertilionis* group) are almost invariably resting inside. The larvae did not survive to the adult stage and have not been identified. The inner surfaces of hollow trees have also been investigated, with negative results.

Rock crevices—While collecting adult *Phlebotomus* from spaces between large rocks, the author spotted one pupal case attached to the underside of one of the rocks, about a foot from the opening. No other pupae nor larvae have since been found in this habitat, despite much searching. As the pupal case was not much above the ground surface, probably the larva merely climbed up from the soil to pupate.

Forest floor; dead leaves.—In rearing *Phlebotomus* in the laboratory, Dr. P. T. Johnson noted that while some species burrowed in the food material, others always remained on top. She therefore thought it likely that these latter species would be found in nature on some surface, such as on decaying leaves and litter on the ground. This ultimately proved to be true for the several species concerned. Through the cooperation of Major R. A. Altman, MSC, U. S. Army, an area within Fort Kobbe Military Reservation was made available to us, where large numbers of *P. panamensis* had often appeared in a horse-baited mosquito trap during the rainy season. Several larvae of *P. panamensis* were obtained from a sample of leaves, debris and soil from a shaded area near the trap. This was followed up 2 days later by the direct examination in the field of moist decaying leaves, which yielded 20 larvae. Additional larvae were found in the same area on a number of other occasions. Later, a few larvae and pupae of *P. pessoana* (closely related to *P. panamensis*) were also found on decaying leaves in two separate areas in the Madden Forest Preserve, where adults of that species were very abundant. The larvae of both species were always on moist, decaying areas of the upper and lower surfaces of the leaves, but if on the lower surfaces, then only

when the leaves were lying loosely. Because of the very long caudal bristles, which in these species are held approximately perpendicular to the body, these larvae are unlikely to occur between tightly packed layers of leaves.

P. trapidoi and *P. ylephiletor* are also surface-feeders in the laboratory, but many searches for larvae on the forest floor in areas where the adults were abundant yielded none until recently (April-July 1960), when particular attention was given to well-decayed leaves and leaf fragments actually on the soil surface. In this short period a total of 38 larvae and pupae were recovered from 16 out of 26 samples of this material in three different areas. The numbers in the positive samples ranged from one to six, most of them apparently either P. *trapidoi* or *P. ylephiletor*, though not all were reared for identification. All of the positive samples were within 5 to 10 feet from the trunk of a large tree where many adults of these two species were resting. Samples taken at the base of such trees have never yielded larvae of either species.

In all, 76 larvae and pupae were recovered from dead leaves on the forest floor, 39 by the flotation method and 37 by direct examination of leaves in the field. Those which were reared to the adult stage comprised five species, *trapidoi, ylephiletor, panamensis, pessoana*, and *galindoi*.

Soil cracks.—During the dry season, from about January to May, the top few inches of the soil become hard and dry and apparently unsuitable as a larval habitat, especially on the Pacific side of Panama. However, soil cracks are also present at that time, and the more moist subsurface soil thus has direct access to the air above, which would permit adults to emerge from moist soil as well as to oviposit there. King (1914) recovered larvae in the Sudan from soil cracks which are apparently the only breeding places in certain regions there. Attempts were made to find immature stages associated with soil cracks during the dry season of 1959 (March) at Cerro Galera, a forested area where both soil cracks and adult *Phlebotomus*, particularly *P. sanguinarius*, were abundant. The cracks here were ½ to 1 inch wide and at least 8 inches deep. The hard clay soil had a thin covering of dry leaves, under which adults of *P. sanguinarius* and *P. gomezi* were found resting during the day. As clumps of the soil along the cracks were broken away and carefully examined, one pupal case of an unknown species was found about 2 inches down from the edge of one of the cracks, approximately where the soil was noticeably more moist. The specimen is unusual in that the caudal bristles of the larval exuvia are relatively short and slightly spatulate, a condition not present in any of the known reared species. To date, no more specimens have been taken in this habitat despite much search.

Other habitats which yielded larvae or pupae were soil under roots, soil around the bases of trees and an ant nest refuse pile near a buttressed tree.

As already noted, Deane and Deane (1957) in Brazil obtained larvae of two species from scrapings of tree trunks. Considerable time has been spent examining this possible habitat, particularly where *P. ylephiletor* was observed resting in large numbers. However, no immature stages were found.

While domestic or semidomestic species occur in the Eastern Hemisphere and South America, none of the species in Panama can be so regarded. Although sand flies will often enter houses or fly under stilted shacks to bite at night, they do not remain and are seldom encountered in houses during the day, even in forested areas where they are abundant. This may be because huts in or near forests are too well ventilated, usually with many openings in the walls and under the eaves, and are thus unsuitable as daytime resting places. For this reason houses as well as animal sheds were largely unexplored as possible breeding places.

Although much is still to be learned, the general picture of sand fly breeding places in Panama has begun to take form. Four of the six man-biting species (*P. trapidoi, P. panamensis, P. ylephiletor* and *P. pessoana*) were found breeding on decaying leaves on the soil surface in well-shaded areas, with no evidence of preference for any particular spot. Whenever larvae were found, many adults of the same species were also observed nearby, either under dead leaves, on tree trunks, or on the underside of green leaves of low plants. If more samples were examined, probably other less common species would also be found there. The immature stages of the other two man-biting species, *P. sanguinarius* and *P. gomezi*, have not been recovered, but it is very likely that these species also oviposit on the forest floor.

In the case of a few species, particularly *P. hamatus, P. ovallesi* Ortiz, and *P. serranus* D. and A., a preference is shown for the sheltered areas between buttresses and at times in large burrows, while the adults of these species seldom use these habitats as daytime resting places. These species, at least, thus apparently seek out such sheltered, dark places in which to oviposit, rather than at random over the forest floor.

A few remarks should be made regarding food habits of *Phlebotomus* larvae as observed in natural habitats. The top layer of soil of the forest floor, and especially between buttresses, contains feces of various animals, such as lizards, which might well be an important supply of food for *Phlebotomus* larvae, although none were actually seen feeding on such material. Fragments of bodies of various arthropods are also numerous on the ground and on dead leaves, and often make up a considerable proportion of the material taken from buttresses. These fragments probably have accumulated from the predatory activities of ants, spiders, bats, etc., inhabiting these places. On one occasion larvae and pupae of *P. serranus* were found on a dead caterpillar taken from a dark, recessed area between buttresses. As all species being reared in the laboratory here readily feed on frag-

ments of dead insects, very possibly such material is quite generally utilized as food in natural habitats.

Parrot (1932) has found dead leaves to be sufficient for the development of *P. papatasi* in Algeria, and this appears to be true also for *P. panamensis* and *P. pessoana* here. As discussed above, larvae of four species have been found on dead leaves and in some cases were actually seen feeding on them or on the micro-organisms growing on them.

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Competition and the Species-Per-Genus Structure of Communities[1]

DAVID PIMENTEL[2]

Department of Entomology, Cornell University, Ithaca, N.Y.

ABSTRACT

The ecological relationship of the 208 taxa which make up the *Brassica oleracea* L. (Cruciferae) community was investigated. Of the total taxa, 63% of the species were members of a genus represented by one species; 21% were members of a genus with two species; 12% were members of a genus with three species; and 4% were members of a genus with four species. After observing the competition and pressure of parasites and predators on competing species in the community, little significance could be attributed to competition and the species per genus structure of communities without additional information concerning natural population dynamics.

Darwin stressed the importance of competition in the evolution of life (Darwin, 1859). He further set forth the principle that competition between related species is more intense because related forms have more similar demands than unrelated forms. This knowledge led Elton (1946) to propose that the number of species per genus in communities should be lower than lists of fauna and flora irrespective of community boundaries. The aim of this investigation was to study the species-per-genus relationship and the competitive interactions through an analysis of the structural and functional organization of the community associated with the plant, *Brassica oleracea* L. (Cruciferae).

The *Brassica oleracea* community has many desirable attributes for ecological study: (a) The community exists in both cultivated and natural habitats. (b) Herbivore-plant, predator-prey, and parasite-host interactions are numerous in the community. (c) Sampling is possible for all the species without destroying or seriously affecting the community. (d) The majority of the herbivorous species have no required alternate host plants. (e) The community is self-sufficient. (f) The trophic plant is relatively stable (biennial). (g) Some control of the nutritional content of the plant is possible. (h) Most animal species can be reared in the laboratory. (i) Easy observation of the behavior of all animals is possible.

Information has been published concerning a few of the individual species members of this cruciferan community. Hering (1932) wrote an exhaustive thesis on the herbivorous insects associated with the plants of the mustard family (Cruciferae). In South Africa, Ullyett (1947) focused his attention on the diamond-back moth, *Plutella maculipennis* Curt., and published an account of the mortality factors influencing its populations. The cabbage worm, *Pieris rapae* (L.), has been thoroughly studied by various workers (Moss, 1933; Muggeridge, 1943; and Richards, 1940). McKinney (1944) investigated the ecology of the cabbage looper, *Trichoplusia ni* (Hbn.). The ecology of the turnip aphid, *Rhopalosiphum pseudobrassicae* (Davis) has been carefully explored by Davis and Satterthwait (1916) and that of the cabbage aphid *Brevicoryne brassicae* (L.) by Prethebridge and Mellor (1936).

While all these studies contribute much to the information about various parts of the cruciferan community, the interactions of these parts within the bounds of the community and the community itself as whole have not been studied.

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METHODS

The aim of this study was to investigate the ecology of the community associated with *B. oleracea* and to study its structure and function as a unit. A major portion of the data reported herein was collected during 1956, and additional data were obtained during the 1957, 1958, and 1959 seasons. The test plots containing *B. oleracea* plants, principally varieties of cabbage, kale, broccoli, and collards, were located in East Ithaca. The test plots ranged in size from 7,500 square feet to 27,000 square feet.

All plots were fertilized at a rate of 2,000 pounds of 5-10-5 per acre and were maintained weed-free. *B. oleracea* plants of the varieties broccoli and collards were allowed to blossom for those animals requiring nectar. Temperature and rainfall data were collected during the study.

Determination of the relationship of the various species to one another in the community was made principally by observation. Many herbivores were caged on leaves to determine whether they would

[1] Accepted for publication July 18, 1960.
[2] Associate Professor of Insect Ecology.

complete their development and to observe their type feeding injury. Samples of the various species were brought into the laboratory to study those parasites which emerged from them. No species was listed as a member of the *B. oleracea* community unless they played some role in it.

RESULTS

A systematic list of the 207 kinds of plants and animals which formed the structure of the *B. oleracea* community is recorded in table 1. Information is given on the function of each taxon and its relative abundance in the community. Density is based on the number of each taxon per 500,000 square inches of *B. oleracea* leaf surface area (see Pimentel 1961 for sampling details). The density figure is an average for the 1957 and 1958 seasons.

The information in figure 1 diagrams the relationships between a number of the taxa of the community. Herbivores were the most abundant. Only the activities of plant feeding, parasitism, and predation are included. Although competition interactions and other types of interferences are not diagrammed, the resulting complexity of association is evident. For this group of taxa, the number of species in the food chain at the various consumer levels is "diamond shaped"—there is 1 plant species, then 8 herbivorous taxa, and, at the peak, 27 first-order carnivores. The decrease is now to six second-order carnivores and last one individual third-order carnivore. Although the number of taxa increases in number up to second-order carnivores, however, if biomass were considered it would decrease from the producer to the last third-order carnivore. The design would follow the "pyramid of numbers" (Elton 1927) pattern.

DISCUSSION

Of the total of 208 taxa present in the community associated with *Brassica oleracea*, 63% of the species were members of a genus represented by one species. A total of 21% of the species were members of a genus with two species; 12% were members of one genus with three species; and 4% were members of one genus with four species. Elton (1946) reported in a survey of 55 animal communities that 66% were members of genera represented by one species. In contrast, only 50% of the species of a faunal list of British insects were members of genera represented by one species. Elton concluded, "The difference in species/genus frequencies between ecological surveys of relatively small parts of any general habitat, and those for faunal lists from larger regions, is attributed to existing or historical effects of competition between species of the same genus, resulting in a strong tendency for the species of any genus to be distributed as ecotypes in different habitats, or if not, to be unable to coexist permanently on the same areas of the same habitat." This analysis was challenged by Williams (1947). Bagenal (1951) studied carefully the arguments of Elton and Williams and suggested that part of the confusion was "based on differences in the meaning of the word 'habitat.'" Williams used habitat to mean extensive areas, but Elton had in mind more restricted areas. According to Bagenal's interpretation, Elton's conclusions were correct but based on unsuitable data.

The conclusions of Elton were based, apparently, on two assumptions. First, competition is a dominant activity in natural populations, and second, taxonomic species are synonymous with ecologic species. Andrewartha and Birch (1954) questioned whether competition is a dominant activity when they proposed that species are rare "by whatever criterion they are judged." In the *B. oleracea* community only three species, *Rhopalosiphum pseudobrassicae*, *Brevicoryne brassicae*, and *Myzus persicae* of the 208 taxa were ever abundant enough for noticeable intra- and interspecific competition (Pimentel, unpublished data). This occurred, however, only in the pure-species stand of *B. oleracea*. In more natural areas these species never became sufficiently abundant for any measureable competition (Pimentel, in press). The competition observed, however, in the populations of these aphids in pure stands was usually of short duration. Weather and other environmental conditions changed rapidly and did not favor one species long. Early in the cool, moist spring the aphids thrived, but then the hot summer weather and carnivore pressure suppressed the aphid populations. During early fall conditions allowed the aphid populations to increase for a short period before the cold destroyed most of the aphids. Thus, in the *B. oleracea* community competition was not a dominant activity, and, in fact, it was an observed rarity.

Evidence gained in this study supports the proposition that parasites and predators tend to preserve balance between species populations and to prevent the extinction of one species by competition. The carnivores were observed to exert greater pressure on the more abundant of the related species (ecologic and morphologic species) than on the less dense species. *Diaeretus rapae* parasitized *M. persicae*, *R. pseudobrassicae* and *B. brassicae*. In general, parasitism rates were higher in the dense species than in the sparse species. For example, during 15 weeks of the 1957 season the following observations were made: a total of 34,854 *B. brassicae*, 1,077 *M. persicae* and 6 *R. pseudobrassicae* were counted per 20,000 square inches of plant area, and the parasitism rates, respectively, were 20%, 4%, and 0%. If the individuals of the aphid species were distributed at random, we would not expect to find this difference in parasitism rates, but they are not distributed at random. Aphids, especially, are distributed in aggregate groups. The most dense aphid populations had the largest colonies, and, of course, these were the easiest to find and were most heavily parasitized. Because the parasites concentrated on the most dense populations, the least dense species was favored.

Table 1.—A list of the taxa which formed the structure of the *Brassica oleracea* community, with information on the role of each in the community.

Taxa	Density	Role[a]	Remarks	Common name
LEPIDOPTERA				
Arctiidae				
Diacrisia virginica Fabr.	1	H	Larvae feed on leaves, [adults on nectar]	Yellow woollybear
Euchromidae				
Cisseps fulvicollis (Hbn.)	1	H	Larvae feed on leaves, [adults on nectar]	
Noctuidae				
Amathes c-nigrum (L.)	1	H	Larvae feed on leaves, [adults on nectar]	Spotted cutworm
Amphipyra tragopodinis L.	1	H	Larvae feed on leaves, [adults on nectar]	
Autographa sp.	1	H	Larvae feed on leaves, [adults on nectar]	
Ceramica picta (Harr.)	1	H	Larvae feed on leaves, [adults on nectar]	Zebra caterpillar
Peridroma saucia (Hbn.)	1	H	Larvae feed on leaves, [adults on nectar]	Variegated cutworm
Polia subjuncta G. and R.	1	H	Larvae feed on leaves, [adults on nectar]	Speckled cutworm
Schinia arcigera Gn.	1	H	Larvae feed on leaves, [adults on nectar]	
Scotogramma trifolii Rott.	1	H	Larvae feed on leaves, [adults on nectar]	Clover cutworm
Trichoplusia ni (Hbn.)	12	H	Larvae feed on leaves, [adults on nectar]	Cabbage looper
Pieridae				
Pieris rapae (L.)	120	H	Larvae feed on leaves, [adults on nectar]	Imported cabbageworm
Pterophoridae				
Oidaematophorus monodactylis L.	1	H	Larvae feed on leaves, [adults on nectar]	
Pyralididae				
Udea rubigalis Guen.	1	H	Larvae feed on leaves, [adults on nectar]	Greenhouse leaf tier
Tortricidae				
Argyrotaenia velutinana Walk.	1	H	Larvae feed on leaves, [adults on nectar]	Red-banded leafroller
Yponomeutidae				
Plutella maculipennis (Curt.)	75	H	Larvae feed on leaves, [adults on nectar]	Diamondback moth
HOMOPTERA				
Aphidae				
Aphis nasturtii (Kltb.)	1	H	Feed on sap	Buckthorn aphid
Aphis fabae Scop.	1	H	Feed on sap	Bean aphid
Brevicoryne brassicae (L.)	9,000	H	Feed on sap	Cabbage aphid
Macrosiphum granarium (Kby.)	2	H	Feed on sap	English grain aphid
Macrosiphum euphorbiae (Thomas)	1	H	Feed on sap	Potato aphid
Myzus persicae (Sulz.)	900	H	Feed on sap	Green peach aphid
Pemphigus sp.	1	H	Feed on sap	
Rhopalosiphum fitchii (Sand.)	1	H	Feed on sap	Apple grain aphid
Rhopalosiphum pseudobrassicae (Davis)	450	H	Feed on sap	Turnip aphid
Sipha agropyrella (HRL)	1	H	Feed on sap	
Cercopidae				
Philaenus leucophthalmus (L.)	3	H	Feed on sap	Meadow spittlebug
Cicadellidae				
Aceratagallia sanguinolenta (Prov.)	1	H	Feed on sap	Clover leafhopper
Draeculacephala antica (Walk.)	1	H	Feed on sap	
Graphocephalus coccinea Forst.	1	H	Feed on sap	
Macrosteles fascifrons (Stål)	1	H	Feed on sap	Six-spotted leafhopper
Cixiidae				
Haplaxius fulvus (Osb.)	1	H	Feed on sap	
Delphacidae				
Delphacodes sp.	1	H	Feed on sap	
Fulgoridae				
Acanalonia bivittata (Say)	1	H	Feed on sap	
Psyllidae				
Aphalara sp.	1	H	Feed on sap	

[a] H stands for herbivore, C for carnivore.

Table 1, *Continued*

Taxa	Density	Role	Remarks	Common name
HEMIPTERA				
Anthocoridae				
Orius insidiosus (Say)	1	H	Feed in blossom	
Miridae				
Lygus lineolaris (P. de B.)	16	H	Feed on sap	Tarnished plant bug
Plagiognathus politus (Uhler)	1	C	Prey on *B. brassicae* and other aphids	
P. politus var. *flaveolus* Knight	1	C	Prey on *B. brassicae* and other aphids	
Poecilocapsus lineatus (Fabr.)	1	H	Feed on sap	Four-lined plant bug
Nabidae				
Nabis alternatus Parshley	1	C	Prey on *B. brassicae* and other aphids	
Nabis ferus (L.)	1	C	Prey on *B. brassicae* and other aphids	
Nabis major (Costa)	1	C	Prey on *B. brassicae* and other aphids	
Pentatomidae				
Cosmopepla bimaculata (Thomas)	1	C	Prey on *Plutella maculipennis* larvae	
Tingidae				
Corythucha marmorata Uhler	1	H	Feed on sap	Chrysanthemum lace bug
Reduviidae				
Zelus sp.	1	C	Prey on aphids	
COLEOPTERA				
Cantharidae				
Podabrus rugulosus Lec.	1	C	Adults prey on *B. brassicae*	
Chrysomelidae				
Diabrotica undecimpunctata howardi Barber	2	H	Adults feed on leaves	Spotted cucumber beetle
Longitarsus sp.	1	H	Adults feed on leaves	
Phyllotreta cruciferae Goeze	400	H	Adults feed on leaves	
Phyllotreta striolata (Fabr.)	1,500	H	Adults feed on leaves	Striped flea-beetle
Psylliodes punctulata Melsh.	800	H	Adults feed on leaves	Hop flea-beetle
Systena blanda Melsh.	1	H	Adults feed on leaves	Pale-striped flea beetle
Coccinellidae				
Adalia bipunctata (L.)	1	C	Prey on aphids and other small animals	Two-spotted lady beetle
Ceratomegilla maculata fuscilabris Deg.	10	C	Prey on aphids and other small animals	
Coccinella trifasciata L.	1	C	Prey on aphids and other small animals	
Coccinella novemnotata Hbst.	1	C	Prey on aphids and other small animals	
Coccinella transversoguttata Fald.	7	C	Prey on aphids and other small animals	Transverse lady beetle
Hippodamia convergens Guér.	10	C	Prey on aphids and other small animals	Convergent lady beetle
Hippodamia tredecimpunctata tibialis (Say)	1	C	Prey on aphids and other small animals	
Neomysia pullata (Say)	1	C	Prey on aphids and other small animals	
Cryptophagidae				
Caenoscelis subfuscata Casey	1	H	Adults feed on decayed plant parts	
Curculionidae				
Calendra minima (Hart)	1	H	Adults feed on leaves	
Ceutorhynchus erysimi (F.)	1	H	Adults feed on leaves	
Ceutorhynchus rapae (Gyll.)	1	H	Adults feed on leaves	Cabbage curculio
Phyxelis rigidus (Say)	1	H	Adults feed on leaves	
Scarabaeidae				
Popillia japonica Newm.	1	H	Adults feed on leaves	Japanese beetle
Scolytidae				
Hylastinus obscurus (Marsh)	1	H	Adults feed on leaves	Clover root borer
Staphylinidae				
Atheta ?festinans Er.	1	C	Adults prey on *P. maculipennis* pupae.	
Baryodma sp.	1	C	Adults prey on *H. brassicae* pupae.	

Table 1, *Continued*

Taxa	Density	Role	Remarks	Common name
DIPTERA				
Agromyzidae				
Agromyza parvicornis Lw.	1	H	Adults feed in blossoms	Corn blotch leaf miner
Ceradontha dorsalis Lw.	1	H	Adults feed in blossoms	
Liriomyza sp.	1	H	Larvae mine leaves and adults feed on nectar	
Asilidae				
Erax aestuans (L.)	1	H	Adults prey on *Hylemyia* sp. and other small Diptera	
Bombyliidae				
Geron (*Empidigeron*) *calvus* Loew	1	H	Adults feed in blossoms	
Calliphoridae				
Pollenia rudis (Fabr.)	1	H	Adults feed in blossoms	Cluster fly
Chironomidae				
Cricotopus sp.	1	H	Adults feed in blossoms	
Chloropidae				
Elachiptera erythropleura Sabr.	1	H	Adults feed in blossoms	
Elachiptera nigriceps (Lw.)	1	H	Adults feed in blossoms	
Hippelates bishoppi Sabr.	1	H	Adults feed in blossoms	
Hippelates particeps (Beck)	1	H	Adults feed in blossoms	
Hippelates plebejus Lw.	1	H	Adults feed in blossoms	
"Madiza" parva (Ad.)	1	H	Adults feed in blossoms	
"Madiza" setulosa (Lw.)	1	H	Adults feed in blossoms	
Oscinella neocoxendis Sabr.	1	H	Adults feed in blossoms	
Oscinella carbonaria (Lw.)	1	H	Adults feed in blossoms	
Oscinella coxendix (Fitch)	1	H	Adults feed in blossoms	
Oscinella frit (L.)	1	H	Adults feed in blossoms	Frit fly
Thaumatomyia glabra (Mg.)	1	H	Adults feed in blossoms	
Culicidae				
Aedes vexans (Mg.)	1	H	Adults feed in blossoms	
Dolichopodidae				
Chrysotus costalis Loew	1	H	Adults feed in blossoms	
Chrysotus sp.	1	H	Adults feed in blossoms	
Condylostylus sp.	1	H	Adults feed in blossoms	
Drosophilidae				
Drosophila busckii Coquillett	1	H	Larvae feed on decayed plants, adults on nectar	
Drosophila quinaria Loew	1	H	Larvae feed on decayed plants, adults on nectar	
Scaptomyza adusta Loew	1	H	Larvae feed on decayed plants, adults on nectar	
Scaptomyza disticha Duda	1	H	Larvae feed on decayed plants, adults on nectar	
Scaptomyza flaveola Meigen	1	H	Larvae feed on decayed plants, adults on nectar	
Ephydridae				
Scatella stagnalis (Fallén)	1	H	Adults feed in blossoms	
Itonididae				
Aphidoletes sp.	15	C	Larvae prey on aphids	
Phytophaga sp.	1	H	Adults feed in blossoms	
Larvaevoridae				
Compsilura concinnata (Mg.)	2	H, C	Larvae parasitize larvae and pupae of *T. ni* and adults feed on nectar	
Phryxe vulgaris (Fall.)	20	H, C	Larvae parasitize larvae and pupae of *P. rapae;* adults feed on nectar	
Lycoriidae				
Bradysia sp.	1	H	Adults feed in blossoms	
Muscidae				
Coenosia (*Limosia*) *nigrescens* Stein	1	H	Adults feed in blossoms	
Coenosia (*Neodexiopsis*) *ovata* Stein	1	H	Adults feed in blossoms	
Coenosia (*C.*) *tigrina* (Fabr.)	1	H	Adults feed in blossoms	

Table 1, *Continued*

Taxa	Density	Role	Remarks	Common name
Hebecnema sp.	1	H	Adults feed in blossoms	
Hylemyia aemene (Walker)	1	H	Adults feed in blossoms	
Hylemyia brassicae (Bouché)	1	H	Adults feed in blossoms	Cabbage maggot
Hylemyia cilicrura (Rond.)	1	H	Adults feed in blossoms	Seed-corn maggot
Hylemyia sp.	1	H	Adults feed in blossoms	
Musca domestica L.	1	H	Larvae feed on decayed plant stems, adults feed on nectar	House fly
Ophyra leucostoma (Wied.)	1	H	Adults feed in blossoms	
Otitidae				
Callopistromyia annulipes (Macq.)	1	H	Adults feed in blossoms	
Sarcophagidae				
Sarcophaga (*Ravinia*) *pusiola* Wulp	1	H	Adults feed in blossoms	
Sarcophaga (*Ravinia*) *stimulans* Walk.	1	H	Adults feed in blossoms	
Sepsidae				
Enicita annulipes (Mg.)	1	H	Adults feed in blossoms	
Sepsis punctum (F.)	1	H	Adults feed in blossoms	
Scatopsidae				
Scatopse fuscipes Mg.	1	H	Adults feed in blossoms	
Sylvicolidae				
Sylvicola alternata (Say)	1	H	Adults feed in blossoms	
Syrphidae				
Allograpta obliqua Say	1	H, C	Larvae prey on aphids and small caterpillars; adults feed on nectar	
Eristalis tenax L.	1	H	Adults feed in blossoms	
Mesogramma marginata Say	1	H, C	Same as *A. obliqua* Say	
Metasyrphus wiedemanni (Johnson)	1	H, C	Same as *A. obliqua* Say	
Sphaerophoria cylindrica Say	11	H, C	Same as *A. obliqua* Say	
Sphaerophoria menthrasti (L.)	4	H, C	Same as *A. obliqua* Say	
Sphaerophoria robusta (Curran)	2	H, C	Same as *A. obliqua* Say	
Tephritidae				
Euaresta bella (Lw.)	1	H	Adults feed in blossoms	
Tipulidae				
Neolimnophila ultima (O.S.)	1	H	Adults feed in blossoms	
HYMENOPTERA				
Braconidae				
Apanteles glomeratus (L.)	21	H, C	Larvae parasitic on larvae of *P. rapae;* adults feed on nectar	
Aphidius nigripes Ashm.	1	H, C	Larvae parasitize *M. persicae;* adults feed on nectar and exudate from aphids wounded during oviposition	
Aphidius (*Lysiphlebus*) *testaceipes* (Cress.)	1	H, C	Larvae parasitize *A. abbreviata;* adults feed as do *Aphidius nigripes*	
Dacnusa scaptomyzae Gah.	1	H, C	Larvae parasitize larvae of *Scaptomyza* spp. Adults feed on nectar	
Diaeretus rapae (McInt.)	400	H, C	Larvae parasitize *B. brassicae, R. pseudobrassicae,* and *M. persicae.* Adults feed on nectar and exudate from oviposition wounds on aphids	
Microplitis plutellae Mues.	4	H, C	Larvae parasitize larvae of *P. maculipennis;* adults feed on nectar	
Opius dimidiatus (Ashm.)	1	H, C	Larvae parasitize larvae of *Liriomyza* spp; adults feed on nectar	

Table 1, *Continued*

Taxa	Density	Role	Remarks	Common name
Praon sp.	12	H, C	Larvae parasitize *M. persicae;* adults feed on nectar and exudate from oviposition wounds	
Trioxys sp.	1	C	Larvae parasitize *A. abbreviata;* adults feed on nectar and exudate from oviposition wounds	
Ceraphronidae				
Conostigmus sp.	1	H, C	Larvae parasitize *Sphaerophoria* larvae; adults feed on nectar	
Lygocerus niger (How.)	1	H, C	Larvae parasitize hymenopteron parasite in aphids; adults feed on nectar	
Cynipidae				
Charips brassicae (Ashm.)	1,200	H, C	Larvae parasitize hymenoptera parasitic in aphids; adults feed on nectar	
Encyrtidae				
Copidosoma truncatellum (Dalm.)	1	H, C	Larvae parasitize *T. ni* larvae; adults feed on nectar	
Eulophidae				
Pediobus sp.	1	C	Larvae parasitize an unidentified aphid	
Tetrastichus rapo (Walk.)	4	H, C	Larvae parasitize *A. glomeratus* larvae; adults feed on nectar	
Tetrastichus sokolowskii Kurdj.	1	H, C	Larvae parasitize *P. maculipennis;* adults feed on nectar	
Formicidae				
Formica fusca L.	1	H	Workers feed on leaf petiole	
Lasius sp.	1	H	Workers feed on aphid honey-dew	
Prenolepis imparis (Say)	1	H	Workers feed on aphid honey-dew	
Halictidae				
Halictus (*Exylaeus*) *pectoralis* Sm.	1	H	Adults feed in blossoms	
Halictus spp.	1	H	Adults feed in blossoms	
Ichneumonidae				
Campoletis sp.	1	H, C	Larvae parasitize larvae of *P. maculipennis;* adults feed in blossoms	
Colpomeria kincaidii (Ashm.).	1	C	Larvae feed as external parasite on *T. laboriosa*	
Diplazon lactatorius (F.)	5	H, C	Larvae parasitize *S. cylindrica, S. menthastri,* and *S. robusta* larvae. Adults feed on nectar	
Horogenes (?) sp.	40	H, C	Larvae parasitize *P. maculipennis;* adults feed on nectar	
Phaeogenes sp.	1	H	Adults feed in blossoms	
Syrphoctonus agilis Cress.	1	H, C	Larvae parasitize syrphid larvae; adults feed on nectar	
Syrphoctonus (?) *compressiventris* (Cress.)	1	H, C	Same as preceding	

Table 1, *Continued*

Taxa	Density	Role	Remarks	Common name
Stenichneumon culpator cincticornis (Cress.)	1	H, C	Larvae parasitize *T. ni* larvae; adults feed on nectar	
Pteromalidae				
Asaphes fletcheri (Crawf.)	100	H, C	Larvae parasitize *M. persicae* and *B. brassicae;* adults feed on nectar	
Hypopteromalus sp.	1	H, C	Larvae parasitize larvae of *T. sokolowskii*	
Pachyneuron allograptae (Ashm.)	1	H, C	Larvae parasitize larvae of *D. laetatorius;* adults feed on nectar	
Pachyneuron siphonophorae (Ashm.)	1	H, C	Larvae parasitize hymenopterons parasitic in aphids; adults feed on nectar	
Tenthredinidae				
Dolerus elderi Kincaid	1	H	Adults feed in blossoms	
Vespidae				
Vespula maculata (L.)	1	C	Adults prey on adult Diptera	
Vespula vulgaris (L.)	1	C	Adults prey on adult Diptera	
NEUROPTERA				
Chrysopidae				
Chrysopa oculata Say (var. *chlorophana* Brum)	1	C	Larvae prey on aphids and small caterpillars	
Chrysopa oculata Say (var. *oculata* Say)	1	C	Larvae prey on aphids and small caterpillars	Golden-eye lacewing
Chrysopa sp. (*plorabunda* group)	1	C	Larvae prey on aphids and small caterpillars	
THYSANOPTERA				
Thripidae				
Frankliniella tritici (Fitch)	1	H	Feed on leaves	
Thrips tabaci (Lindeman)	1	H	Feed on leaves	
ORTHOPTERA				
Acrididae				
Dissosteira carolina (L.)	1	H	Feed on leaves	
Melanoplus bivittatus (Say)	1	H	Feed on leaves	
CORRODENTIA				
Psocidae				
Blaste "quietus" Chapman, nec Hagen	1	H	Feed on leaves	
COLLEMBOLA	30	H	Feed on leaves	
ISOPODA				
Oniscidae				
Armadillo sp.	1	H	Feed on fresh and decayed plants	
ACARINA				
Erythraeidae				
Leptus sp.	2	C	Nymphs prey on eggs of *T. ni, M. persicae, B. brassicae,* on *M. marginata* adults and on spiders	
ARACHNIDA				
Agelenidae				
Agelenopsis sp.	1	C	Prey on small invertebrates	
Clubionidae				
Clubiona sp.	1	H, C	Prey on small invertebrates	
Clubiona obesa Hertz.	1	C	Prey on small invertebrates	
Linyphiidae				
Meioneta sp.	3	C	Prey on small invertebrates	
Lycosidae				
Lycosa helluo Walckenaer	1	C	Prey on small invertebrates	

Table 1, *Concluded*

Taxa	Density	Role	Remarks	Common name
Pardosa sp.	1	C	Prey on small invertebrates	
Micryphantidae				
Erigone blaesa Crosby and Bishop	1	C	Prey on small invertebrates	
Hypselistes florens Cambridge	1	C	Prey on small invertebrates	
Philodromus sp.	1	C	Prey on small invertebrates	
Xysticus sp.	1	C	Prey on small invertebrates	
Tetragnathidae				
Tetragnatha laboriosa Hentz.	1	C	Prey on small invertebrates	
Theridiidae				
Theridion frondeum Hentz.	3	C	Prey on small invertebrates	
Thomisidae				
Misumenops asperatus Hentz.	1	C	Prey on small invertebrates	
PHALANGIDA				
Phalangodidae				
Phalangium opilio L.	1	H, C	Feed on small invertebrates and plant material	
STYLOMMATOPHORA				
Limacidae				
Deroceras laeve (Muller)	20	H	Feed on leaves	Slug
Deroceras reticulatum (Muller)	20	H	Feed on leaves	Slug
Succineidae	1	H	Feed on leaves	Snail
RODENTIA				
Cricetidae				
Microtus p. pennsylvanicus (Ord.)	1	H, C	Feed on stems and leaves and lepidopteran pupae	Field mouse
ANURA				
Bufonidae				
Bufo americanus Holb.	1	C	Prey on small invertebrates	
PASSERIFORMES				
Fringillidae				
Melospiza melodia (Wilson)	1	C	Prey on *P. rapae* and *T. ni* larvae	Song sparrow
Spizella passerina (Bechstein)	1	C	Prey on *T. ni* and *P. rapae* larvae	Chipping sparrow
Icteridae				
Agelaius phoeniceus (Wilson)	1	C	Prey on *P. rapae* and *T. ni*	Red-winged blackbird
Ploceidae				
Passer domesticus (L.)	1	C	Prey on *P. rapae* and *T. ni*	English sparrow
EUMYCETES				
Phycomycetes				
Empusa aphidis Hoff.	20	C	Parasitize *B. brassicae*, *R. pseudobrassicae*, and *M. persicae*	Fungus
Entomophthora sphaerosperma Fres.	1	C	Parasitize *P. rapae* and *T. ni*	Fungus
Entomophthora sp.	1	C	Parasitize coccinellid and pupa	Fungus
EUBACTERIALES[b]				
Micrococcaceae				
Micrococcus pieridis Bur.	1	C	Parasitize *P. rapae* larvae	Bacterium
VIRALES[b]				
Borrelinaceae				
Borrelinavirus spp.	1	C	Parasitize larvae of *T. ni* and *Autographa* sp.	Polyhedrosis virus
Paillotellavirus pieris (Paillot)	1	C	Parasitize *P. rapae* larvae	Granulosis virus

[b] Counted as number of individual host infections.

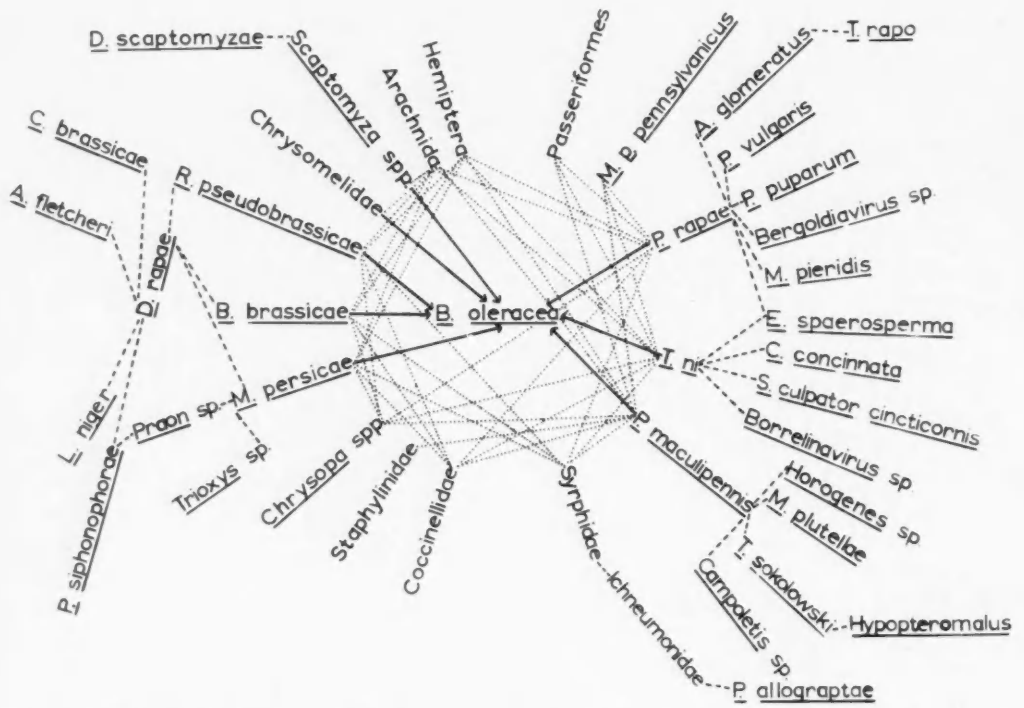

FIG. 1.—The ecologic relationships, herbivorous (——), parasitic (-----), and predaceous (.....), between a number of the more abundant taxa of the community.

This principle is also illustrated with three species of *Scaptomyza*, *S. adusta*, *S. disticha*, and *S. flaveola*, which were all parasitized by one parasite, *Dacnusa scaptomyzae*. Three additional species, *Sphaerophoria cylindrica*, *S. menthastri*, and *S. robusta*, were all parasitized by *Diplazon laetatorius*. Predators behaved in a manner similar to the parasites.

Elton's second assumption, that taxonomic species are synonymous with ecologic species, needs careful consideration when analyzing the species-per-genus ratio in communities. The complexity of this problem is well illustrated by some of the species in the *B. oleracea* community. Before 1914, *B. brassicae* and *R. pseudobrassicae* were considered as one species, namely *Aphis brassicae* L. Then Davis (1914) detected a difference between the two and recognized them as two species, *Aphis brassicae* and *Aphis pseudobrassicae* Davis. Subsequently, *Aphis brassicae* was placed in a new genus, *Brevicoryne* (Das, 1918), and then in 1924 Takahashi placed *Aphis pseudobrassicae* in the genus *Rhopalosiphum*. On the basis of physiologic and ecologic requirements, *R. pseudobrassicae* is more similar to *B. brassicae* than *R. pseudobrassicae* is to other species of *Rhopalosiphum*. Morphologically, *B. brassicae* and *R. pseudobrassicae* are very similar as evidenced by the fact that taxonomists classified them as one until recently.

Our system of taxonomic classification lacks exactness, because the number of species assigned to any one genus depends to a great extent upon the discrimination of the taxonomist. Some taxonomists assign many species per genus while others do the opposite. Attention certainly should be given to differences which sometimes exist between a taxonomic species and an ecologic species.

In conclusion, considering the intensity of competition in natural populations, the pressure of parasites and predators in competing species, and taxonomic methods, little significance can be attributed to the fact that 63% of the species were members of genera represented by one species in the *B. oleracea* community. More information concerning natural population dynamics and the structure of communities is necessary for an evaluation of the species-per-genus ratio in communities.

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A Generic Key to the Nymphs of North American Lygaeidae (Hemiptera-Heteroptera)[1]

MERRILL H. SWEET and JAMES A. SLATER

Department of Zoology and Entomology, University of Connecticut, Storrs

ABSTRACT

This key includes the fifth-instar nymphs of 53 of the Nearctic genera of Lygaeidae, together with the tribes and subfamilies that they represent. Orsillinae, Ischnorhynchinae, and Cyminae are considered as definite subfamilies, and recent changes in the tribal classification of the Megalonotinae are incorporated. Stress is laid on the value of the nymphal stages in systematic studies of this family.

A full decade has passed since Slater (1951) published a preliminary key to the genera of lygaeid nymphs. During this period a great deal of important material has accumulated, and it is now possible to present a more mature key to a much larger number of genera in their last nymphal stage.

This paper is based upon 89 known species, representing 54 genera of Lygaeidae, as compared with only 26 genera keyed in Slater (1951). Thus it will be appreciated that the present key includes most of the genera found north of Mexico. Nymphs of the following genera are still unknown and therefore are great desiderata: *Cymoninus, Dycoderus, Caenopamera, Zeropamera, Exptochiomera, Valonetus, Valtissius, Tomopelta, Tempyra, Thylochromus,* and *Cistalia.*

The accumulation of material has come from several places, but the major additions since 1951 have been from two sources: First, from the detailed and meticulous western collecting of Mr. P. D. Ashlock, who has made available to us representatives of many rare, ground-living, western genera which otherwise could not have been included; Second, from the material obtained during the bionomic studies upon the Megalonotinae now being carried on by the senior author. This additional material enables us to present a key which we hope is not only workable, but is in large part based upon natural units. We have, therefore, utilized trichobothria, abdominal segmentation, and similar features that are now widely used in the classification of the family.

The nymphs are admirable material for study in this family. The trichobothria, abdominal segmentation, and spiracular arrangements often are very difficult to see in the adult insects. Sometimes adults must be dissected and cleared for accurate determination. In the nymphs, by contrast, all of these features usually are very clearly delineated, and their condition can be ascertained at a glance. This ease of study, together with the use of abdominal sutures, abdominal scent-gland characters, head sutures, etc., compensates in large part for the lack of wing venation and genitalia. Indeed, the classification categories of the Lygaeidae must, in the future, be based in part upon nymphal material before we can hope to have a truly mature classification.

Within recent years several major changes have been made in the higher classification of the Lygaeidae. Southwood and Leston (1959) transferred the Cymini from the Lygaeidae to the Berytinidae—a classification which may prove valid, but which is not documented in their book and is not adopted here. The nature of the scent-gland arrangement in the Cyminae would indicate their isolated

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position with respect to the rest of the Nearctic Lygaeidae.

Scudder, in several papers, and Southwood and Leston (1959) have treated the Ischnorhynchinae as a tribe within the Orsillinae, rather than within the Cyminae where they were placed by Stål and other older authors. Usinger and Ashlock (1959), however, discussed the relationships of the two taxa and believed, with good documentation, that the Ischnorhynchinae are worthy of subfamily status distinct from both the Orsillinae and the Cyminae. We have treated the Ischnorhynchinae here as a distinct subfamily, and the nymphal characters would seem to substantiate this distinction. *Kleidocerys*, for example, possesses three dorsal abdominal scent glands, a condition not found in either the Orsillinae or the Cyminae. However, the Neotropical genus *Polychisme*, which is also considered to be an ischnorhynchine, possesses only two dorsal scent glands. Barber (1956) and Scudder (1957a) have treated the group of genera allied to *Ninus* Stål as a tribe Ninini in the Cyminae, and we have adopted this classification here.

In a separate paper (Slater and Sweet 1961) we are proposing certain changes in the tribal classification of the subfamily Megalonotinae. These are based to a considerable extent upon characteristics found in the nymphs, and agree in large part with the proposals projected by Putchkov (1958). Because these changes, coming soon after the major modifications proposed by Scudder (1957), may prove confusing to some students of the group, we summarize them here as follows:

1. The erection of the tribe Plinthisini to contain the genus *Plinthisus* with its subgenera *Isioscytus* and *Plinthisomus*.
2. Elevation of three subtribes of Scudder's Rhyparochromini to tribal status (Gonianotini, Megalonotini, and Myodochini).
3. Resurrection in a restricted sense of Stål's Beosini to contain certain elements placed by Scudder in the Rhyparochromina.

The following table will show the equivalent units of the three systems. Although the Slater and Sweet system is not based wholly upon nymphal characters, many of the criteria important for tribal distinctions can be abstracted from our key.

This key is based upon nymphs of the fifth, or last, nymphal instar. We have found that it will work for third and fourth instars also, in most cases where material was available for testing. When using the key, care should be exercised in measuring the maximum lengths of tarsal segments. Also, the head should be fully exserted before judgment is passed upon the nature of the epicranial sutures. Other points that must be remembered are that in the Heteroptera the first abdominal sternum is not visible, so that the apparent basal segment is in reality sternum 2, and that the first abdominal spiracle is absent in the Lygaeidae.

Specimens of all species have been deposited in the Slater collection at the University of Connecticut.

GENERIC KEY TO THE FIFTH-INSTAR NYMPHS OF NEARCTIC LYGAEIDAE

1. Suture between abdominal sterna 4 and 5 straight and reaching connexivum; two pairs of scent-gland pores present on dorsum of abdomen.....2
   Suture between abdominal sterna 4 and 5 curving anteriorly, not reaching connexivum (see fig. 6); or if suture straight, then three abdominal scent-gland pores, between terga 3 and 4, 4 and 5, and 5 and 6.....18
2. Abdominal spiracles 7 and 8 dorsal.....3
   Abdominal spiracles 7 and 8 ventral.....12
3. Dorsal scent-gland pores present between abdominal terga 4 and 5, and 5 and 6.....4
   Dorsal scent-gland pores present between abdominal terga 3 and 4, and 4 and 5 (CYMINAE).....10
4. Each pair of dorsal scent-gland pores surrounded by a distinct, subcircular, dark, sclerotized plate; color of wing pads solid brown (LYGAEINAE).....5
   Each pair of dorsal scent-gland pores with at most a very thin dark ring around each individual opening; wing pads mottled or striped (ORSILLINAE) 7
5. Epicranial stem absent, epicranial arms meeting just before posterior margin of head (head must be fully exserted to see this character); width across eyes much exceeding length of head (0.98: 0.70 mm.).....**Lygaeospilus** Barber
   L. tripunctatus (Dallas)
   Epicranial stem present; width across eyes less than length of head.....6
6. Anterior lobe of pronotum bearing two raised, dark calli; labium not surpassing abdominal sternum 2, labial segment 3 not surpassing middle coxae .....**Lygaeus** Fabricius, s. latu
   L. kalmii Stål, *L. lateralis* Dallas, *L. hospes* (L.).
   Pronotum smooth, lacking raised calli; labium reaching abdominal sternum 4 or 5, labial segment 3 surpassing abdominal sternum 2....**Oncopeltus** Stål
   O. fasciatus (Dallas)
7. Labium relatively short, never surpassing hind coxae

Table 1.—Equivalent units of the Megalonotinae in three systems of classification.

Stål, 1872-74	Scudder, 1957	Slater and Sweet
Myodocharia	Subtr. Plociomerina	Myodochini
Beosaria	Rhyparochromini, part	Beosini, s. str.
	Stygnocorini, part	
Rhyparochromaria	Subtr. Rhyparochromina	Megalonotini, s. str.
Lethaearia	Lethaeini	Lethaeini
Drymaria	Drymini	Drymini
Gonianotaria	Subtr. Gonianotina	Gonianotini
Cleradaria	Stygnocorini, s. latu	Cleradini, s. latu
		Plinthisini

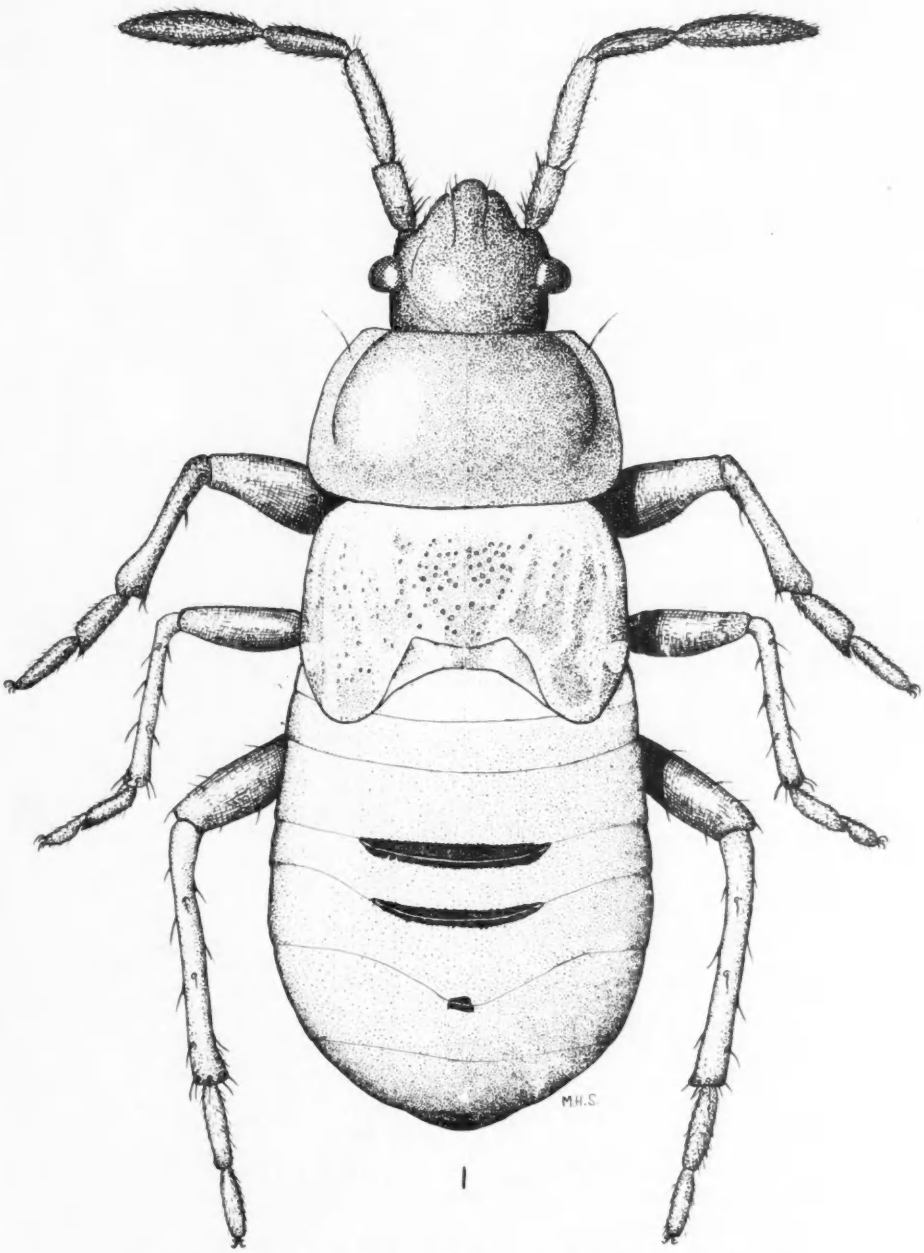

FIG. 1—*Cryphula parallelogramma* Stål, fifth-instar nymph. Dorsal view.

and often only slightly surpassing middle coxae; segments of hind tarsus subequal.....8
Labium long, surpassing abdominal sternum 3; basal segment of hind tarsus shorter than distal one (0.09: 0.14 mm.).....9

8. Pronotum with conspicuous longitudinal stripes; length of head less than width across eyes (0.80: 1.03 mm.).....**Nysius** Dallas
N. angustatus Uhler, *N. ericae* (Schill.)
Pronotum heavily mottled but never striped; length of head subequal to width across eyes (1.04: 1.03 mm.).....**Ortholomus** Stål
O. scolopax (Say)

9. Interocular distance less than length of antennal

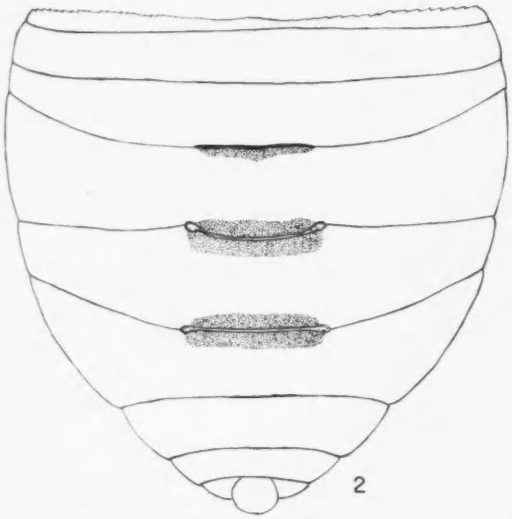

FIG. 2.—*Antillocoris minutus* (Bergroth), fifth-instar nymph. Dorsal view of abdomen.

segment 4 (0.50: 0.55 mm.); fore femora not spinose.....**Orsillacis** Barber
O. productus Barber

Interocular distance greater than length of antennal segment 4 (0.72: 0.52 mm.); fore femora spinose .....**Belonochilus** Uhler
B. numenius (Say)

10. Head, pronotum, and wing pads impunctate; sparsely clothed with long hairs; antennae long, segment 2 longer than length of head; width of head across eyes greater than basal width of pronotum (NININI) .....**Ninus** Stål
N. insignis Stål (not Nearctic, but *Cymoninus notabilis* (Dist.) of Florida will probably key out here)

Head, pronotum, and wing pads heavily punctate; nearly nude; antennae short, segment 2 less than one-half length of head; width of head across eyes less than basal width of pronotum (CYMINI) 11

11. Tylus elongate and punctate, reaching basal one-third of antennal segment 2; labium not surpassing mesosternum, labial segment 2 not reaching front coxae.....**Arphnus** Stål
A. tristis Van Duzee, *A. coriacipennis* Stål

Tylus short, impunctate, barely if at all surpassing antennal segment 1; labium surpassing metasternum, labial segment 2 reaching front coxae .....**Cymus** Hahn
C. angustatus Stål, *C. discors* Horváth, *C. luridus* Stål, *C. robustus* Barber.

12. Spiracles on abdominal segments 3 and 4 dorsal; fore femora rarely incrassate or armed beneath....13

Spiracles 3 and 4 ventral; fore femora incrassate and armed beneath.....16

13. Spiracles on abdominal segments 5 and 6 ventral; spiracle absent on 8; sutures between abdominal terga 4 and 5, and 5 and 6, curving strongly caudad from lateral margins to meson; abdominal tergum 7 narrow and unsclerotized (GEOCORINAE).....14

Spiracles 5 and 6 dorsal; spiracle present on 8; sutures between abdominal terga 4 and 5, and 5 and 6, straight, or only slightly curved caudad to the meson; abdominal tergum 7 broad, with a mesal sclerotized plate (BLISSINAE).....15

14. Eyes very prominent, not in contact with anterolateral margins of pronotum; interocular space at most 2½ times width of an eye; scent-gland plates narrow, but oval; pronotum black, vertex of head dull testaceous.....**Hypogeocoris** Montandon
H. piceus (Say)

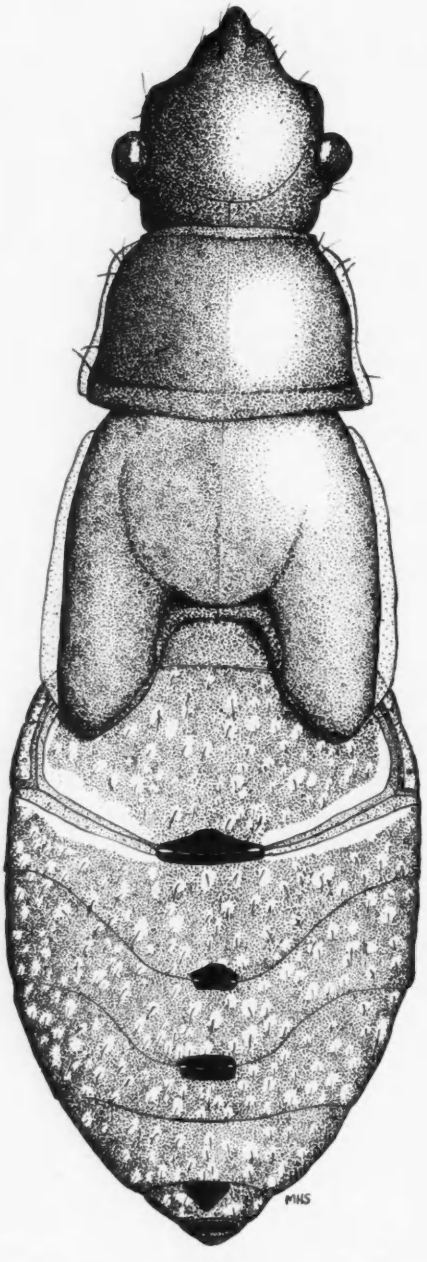

FIG. 3.—*Ligyrocoris diffusus* (Uhler), fifth-instar nymph. Dorsal view.

Eyes less prominent, usually virtually in contact with anterolateral margins of pronotum; interocular space 3 times width of an eye; scent-gland plates constricted mesally into dumb-bell shapes; pronotum variously colored, if black, the vertex of head concolorous ..... **Geocoris** Fallén
G. uliginosus Say, *G. u. limbatus* Stål, *G. bullatus* Say.

15. Body slender, total length at least 3 times maximum width across abdomen; abdominal terga 3, 4, 5, and 6 subequal in width, abdominal tergum 2 narrowed ..... **Ischnodemus** Fieber
I. macer Van Duzee, *I. falicus* (Say)

Body ovoid, total length less than twice width across abdomen; abdominal tergum 2 widest, posterior segments becoming progressively narrower ..... **Blissus** Burmeister
B. leucopterus (Say), *B. mixtus* Barber, *Blissus* sp.

16. Epicranial arms not meeting posteriorly, widely separated at posterior margin of head; spiracle 2 dorsal; fore femora but slightly swollen, with one spine near apex; abdominal segment 8 unsclerotized and colored like segment 7 (OXYCARENINAE) ..... **Crophius** Stål
C. disconotus (Say), *C. angustatus* Van Duzee.

Epicranial arms meeting posteriorly; spiracle 2 ventral; fore femora incrassate and armed beneath with many spines; abdominal segment 8 covered above and below with dark, sclerotized plates (PACHYGRONTHINAE) 17

17. Epicranial stem absent, epicranial arms meeting at posterior margin of head; head and thorax impunctate; antennal segment 1 not surpassing apex of tylus (TERACRINI) ..... **Phlegyas** Stål
P. abbreviatus (Uhler)

Epicranial stem present; head and thorax punctate; antennal segment 1 considerably surpassing apex of tylus (PACHYGRONTHINI) ..... **Oedancala** Amyot and Serville
O. dorsalis (Say), *O. cubana* Stål, *O.* notata Stål, *O. acuminata* Slater, *O. meridionalis* Stål, *O. crassimana* (Fabr.)

18. All abdominal spiracles dorsal; epicranial stem absent (ISCHNORHYNCHINAE) ..... **Kleidocerys** Westwood
K. resedae (Panzer), *K. obovatus* (Van Duzee)

Abdominal spiracles 5 to 8 ventral; epicranial stem present, though sometimes very short 19

19. Suture between abdominal sterna 4 and 5 straight, reaching connexivum; anteriormost scent gland with a single, circular opening between terga 3 and 4, other dorsal scent glands with two openings each (HETEROGASTRINAE) ..... **Heterogaster** Schilling
Heterogaster behrensi Uhler

Suture between sterna 4 and 5, with few exceptions, curving anteriorly and not reaching lateral margin; or, if suture straight, then with either two scent-gland openings or none between terga 3 and 4 (MEGALONOTINAE) 20

20. Suture between abdominal terga 3 and 4 simple, not furcate laterally (fig. 1); lateral margins of pronotum and wing pads carinate or thickly explanate and opaque; scent gland between abdominal segments 3 and 4 sometimes absent; abdomen usually unicolorous 21

Suture between terga 3 and 4 furcate laterally and margined with thickened, depressed cuticle (fig. 3); lateral margins of pronotum and wing pads usually thinly explanate and pale translucent (fig. 3); scent glands always present, and widest, between terga 3 and 4; abdomen frequently with conspicuous white spots or bands 31

21. All abdominal spiracles ventral; abdominal integument pale red; abdominal scent-gland pores between terga 4 and 5 separated by at least two-thirds the interocular width 22

At least spiracle 4 dorsal; abdominal integument dark-colored and heavily sclerotized, or (*Emblethis*) mottled fuscous; scent-gland pores between terga 4 and 5 separated by less than one-half interocular width 26

22. Suture between abdominal sterna 4 and 5 complete, reaching lateral margins of abdomen; posterior two trichobothria on sternum 5 placed one directly above the other (fig. 5) (PLINTHISINI) ..... **Plinthisus** Stephens
P. martini Van Duzee, *P. compactus* Uhler.

Suture between abdominal sterna 4 and 5 curving anteriorly and not attaining lateral margins of abdomen; posterior two trichobothria on sternum 5 not placed one directly above the other (figs. 4-7) (LETHAEINI) 23

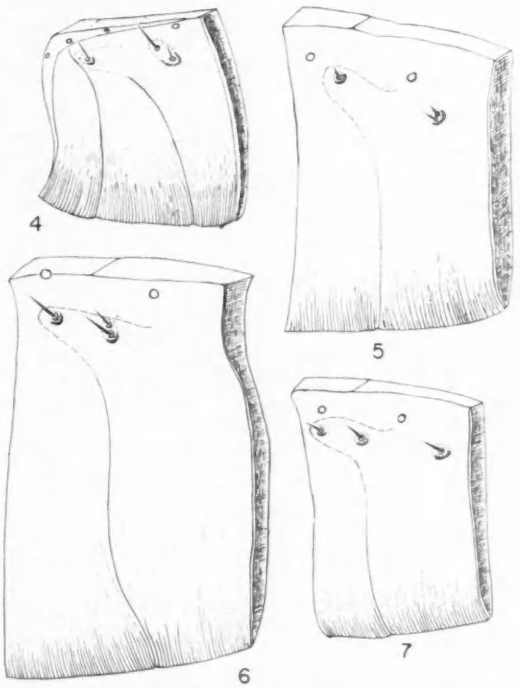

FIG. 4.—*Antillocoris minutus* (Bergroth), adult. Lateral view of anterior abdominal segments. FIGS. 5-7.—Lateral views of fourth and fifth abdominal segments of fifth-instar nymphs of *Ozophora picturata* Uhler (FIG. 5), *Drymus unus* (Say) (FIG. 6), and *Cryphula parallelogramma Stål* (FIG. 7).

23. Scent-gland pores absent between abdominal terga 3 and 4, in fifth instar represented by a thin, linear plate on anterior margin of tergum 4 (fig. 2); posterior two trichobothria of segment 5 grouped together near spiracle which is located on posterior third of segment (fig. 4); total length less than 2 mm ..... **Antillocoris** Kirkaldy
A. minutus (Bergroth)

Scent-gland pores present between abdominal terga 3 and 4; posterior trichobothria on segment 5 in linear arrangement and each separate from the others (fig. 7); total length usually more than 3 mm. 24

24. Scent-gland pores between terga 5 and 6 as widely separated from one another as those between terga 4 and 5; scent-gland pores between terga 3 and 4 separated from one another by two-thirds inter-

ocular width; no mesal sclerotized plates present on sterna 7 and 8.....**Cligenes** Distant
Cligenes n. sp.

Scent gland between abdominal terga 5 and 6 very small, without lateral pores, in contrast with widely separated pores between terga 4 and 5 (fig. 1); distance separating scent-gland pores between terga 3 and 4 greater than interocular width; sclerotized plates present on abdominal sterna 7 and 8 25

25. Epicranial arms concave to meson (fig. 1); basal segment of hind tarsus definitely longer than distal (0.35: 0.25 mm.); first antennal segment shorter than third (0.28: 0.39 mm.); wing pads punctate.....**Cryphula** Stål
C. parallelogramma Stal

Epicranial arms convex to meson; segments of hind tarsus subequal in length (0.25: 0.23 mm.); antennal segments 1 and 3 subequal (0.33: 0.35 mm.); wing pads impunctate.....**Xestocoris** Van Duzee
X. nitens Van Duzee

26. Abdominal scent-gland pores present between terga 3 and 4; spiracle of segment 3 dorsal (MEGALONOTINI) 27

Abdominal scent-gland pores absent between terga 3 and 4; spiracle of segment 3 ventral (GONIANOTINI) 28

27. Scent-gland pores between abdominal terga 4 and 5 closer together than those between terga 3 and 4, or between 5 and 6; labial segments 2 and 3 subequal (0.45: 0.44 mm.).....**Megalonotus** Fieber
M. chiragra (Fabricius)

Scent-gland pores between terga 5 and 6 closest together, these and the openings between terga 4 and 5 almost equally separated; labial segment 2 longer than 3 (0.40: 0.30 mm.)....**Sphragisticus** Stål
S. nebulosus (Fallén)

28. Body light-mottled-fuscous; abdomen relatively lightly sclerotized; antennal segments 2 and 3 with strong bristles; a row of short setae present on explanate lateral margins of pronotum.....**Emblethis** Fiber
E. vicarius Horváth

Body dark-colored; abdomen strongly and heavily sclerotized; antennal segments 2 and 3 without strong bristles, as pilose as segment 4; pronotum with at most a few scattered setae.....29

29. Lateral margins of pronotum slightly sinuate, nearly parallel; length of pronotum more than three-fifths width of pronotum (0.75: 1.25 mm.); interocular width subequal to length of antennal segment 2 (0.59: 0.55 mm.)....**Malezonotus** Barber
M. angustatus (Van Duzee), *M. barberi* Ashlock, *Malezonotus* spp.

Lateral margins of pronotum convex, converging anteriorly; pronotum about one-half as long as wide (0.89: 1.71 mm.); interocular space wider than length of antennal segment 2 (0.70: 0.55 mm.) 30

30. Segments of hind tarsus subequal; length of pronotum three-fourths width of head across eyes (0.75: 0.98 mm.); antennal segments all dark fuscous .....**Trapezonotus** Fieber
T. arenarius (Linnaeus)

Basal segment of hind tarsus longer than distal one (0.43: 0.35 mm.); length of pronotum more than three-fourths width of head across eyes (0.90: 1.00 mm.); antennal segments 2 and 3 flavescent, 1 and 4 dark.....**Delochilocoris** Bergroth
D. umbrosus (Distant)

31. All three trichobothria on sternum 5 located anterior to spiracle (fig. 6) (DRYMINI).....32

Posterior pair of trichobothria on sternum 5 located posterious to spiracle (fig. 5).....36

32. Spiracle on abdominal segment 4 lateral in position, the others ventral (fig. 6); fore femora with one spine; lateral margin of abdomen pale yellow .....**Drymus** Fieber
D. unus (Say), *D. crassus* Van Duzee

Spiracle of abdominal segment 4 ventral, in line with other spiracles; fore femora with many spines; lateral margin of abdomen not yellow.....33

33. Suture between sterna 4 and 5 nearly straight, reaching connexivum; body strongly flattened.....**Gastrodes** Westwood
G. pacificus (Provancher), *G. conicola* Usinger

Suture between sterna 4 and 5 strongly curving anteriorly, not reaching connexivum; body not strongly flattened.....34

34. Antennal segment 1 barely surpassing tylus, segment 2 subequal to or shorter than segment 4; wing pads mottled fuscous and white; less than 4.5 mm. in length.....**Scolopostethus** Fieber
S. thomsoni Reuter, *S. diffidens* Horváth, *S. atlanticus* Horváth, *Scolopostethus* sp.

Antennal segment 1 considerably surpassing tylus, segment 2 distinctly longer than 4; wing pads solid fuscous; more than 5.5 mm. in length.....35

35. Fore femora with one row of spines; head longer than pronotum (1.06: 0.90 mm.).....**Togodolentus** Barber
T. wrighti (Van Duzee)

Fore femora with two rows of spines, the outer row shorter; head shorter than or subequal in length to pronotum (at most 0.92: 0.90 mm.) .....**Eremocoris** Fieber
E. ferus (Say)

36. Abdominal spiracles all ventral (CLERADINI).....37

At least spiracle on abdominal segment 4 dorsal.....38

37. Pronotal collar absent; segments of hind tarsi subequal; fore femora mutic.....**Stygnocoris** Douglas and Scott
S. rusticus (Fallén), *S. pedestris* (Fallén)

Pronotal collar present; basal segment of hind tarsus twice as long as distal one; fore femora spinose .....**Ozophora** Uhler
O. picturata Uhler, *O. concava* (Distant)

38. Spiracles of abdominal segment 2 ventral; pronotal collar absent (BEOSINI).....39

Spiracles of abdominal segment 2 dorsal; often with a pronotal collar (MYODOCHINI).....40

39. Labium reaching middle coxae; body ovoid; third antennal segment shorter than width of interocular space (0.43: 0.52 mm.); fore femora strongly incrassate, with three or four spines.....**Peritrechus** Fieber
P. saskatchewanensis Barber, *P. fraternus* Uhler, *P. tristis* Van Duzee

Labium reaching hind coxae; body elongate; third antennal segment longer than width of interocular space (0.75: 0.69 mm.); fore femora only slightly more incrassate than hind femora, and with one spine.....**Uhleriola** Horváth
U. floralis (Uhler)

40. Segments of hind tarsi subequal in length (0.22: 0.20 mm.); pronotal collar absent or indistinct; fore femora at most with a few setalike spines 41

Basal segment of hind tarsus distinctly longer than distal; a distinct pronotal collar present; fore femora often strongly spinose.....45

41. Scent-gland plates broad, covering at least one-half of mesal area of tergum 4; sternum 7 almost entirely covered by a sclerotized plate.....42

Scent-gland plates narrow, covering considerably less than one-half of mesal area of tergum 4; sternum 7 with at most a small mesal plate.....43

42. Scent-gland plates covering two-thirds of mesal area of tergum 4; fore femora not spinose; a large, sclerotized plate present on sternum 6; abdomen uniformly pale red; head and pronotum light fuscous; length less than 2 mm.....**Neosuris** Barber
N. castanea (Barber)

Scent-gland plates covering one-half of mesal area of tergum 4; fore femora with one spine; no sclerotized plate present on abdominal sternum 6; abdomen transversely banded with red and white;

head and pronotum piceous; length more than 2.5 mm.....**Kolenetrus** Barber
K. planus (Distant)

43. Antennal segments 2 and 4 subequal in length (0.36: 0.35 mm.); fore femora bearing three setalike spines; vertex of head with flavescent mesal area; abdomen predominantly gray.....**Carpilis** Stål
C. consimilis Barber

Antennal segment 2 considerably shorter than 4 (0.35: 0.43 mm.); fore femora mutic; head unicolorous; abdomen predominantly red.....44

44. Abdominal sternum 7 unsclerotized; antennal segment 2 more than two-thirds as long as 4 (0.38: 0.45 mm.); antennal segment 3 subcylindrical and of same thickness as 4, segment 4 uniformly pilose with fine, pale hairs.....**Ptochiomera** Say
P. nodosa Say

Sternum 7 with a sclerotized mesal plate; antennal segment 2 about one-half as long as 4 (0.21: 0.41 mm.); segment 3 clavate and nearly twice as thick as 2, segment 4 with long, dark hairs on proximal half.....**Sisamnes** Distant
S. clavigera (Uhler)

45. Epicranial stem much longer than epicranial arm; abdomen with dark, longitudinal stripes.....**Myodocha** Latreille
M. serripes Olivier

Epicranial stem shorter than epicranical arm; abdomen transversely striped, or unstriped.....46

46. Lateral margin of pronotum thickly explanate and opaque; abdomen densely pilose with long hairs.....47

Lateral margin of pronotum thinly explanate and pale-translucent (fig. 3); abdomen sparsely pilose with short hairs.....48

47. Head constricted caudad into a short "neck"; lateral margins of wing pads thinly explanate and pale-translucent; two rows of spines on fore femora; a mesal sclerotized plate present on tergum 7; abdomen with a white band on sternum 4, and not uniformly spotted.....**Heraeus** Stål
H. plebejus Stål

Head not constricted caudad into a short "neck"; lateral margins of wing pads thickly explanate and opaque; one spine on fore femora; no sclerotized plate on tergum 7; abdomen not banded, but thickly and uniformly covered with fine, white spots.....**Perigenes** Distant
P. constrictus (Say)

48. Abdomen thickly and uniformly covered with white spots on a dark background (fig. 3), occasionally with a white area on terga 6 and 7; width of pronotum at base greater than width of head across eyes; fore femora often with one row of spines.....49

Abdomen not uniformly spotted, and never with a white area on terga 6 and 7; width of pronotum at base frequently subequal to or less than width of head across eyes; fore femora usually with two rows of spines.....50

49. Fourth labial segment three-fourths as long as third; basal segment of hind tarsi at most twice as long as distal (except in *latimarginatus*); some species of subgenus *Pseudopamera* with white mesal area on terga 6 and 7; abdomen frequently reddish.....**Ligyrocoris** Stål
L. (s.s.) *sylvestris* (Linnaeus), *L. diffusus* Uhler, *L. depictus* Barber, *L. latimarginatus* Barber; *L. (Pseudopamera) aurivillianus* (Distant), *L. (P.) nitidicollis* Stål; *Ligyrocoris* spp.

Fourth labial segment one-half as long as third; basal segment of hind tarsi considerably more than twice as long as distal (0.85: 0.35 mm.); no white area on terga 6 and 7; abdomen fuscous.....**Zeridoneus** Barber
Z. costalis (Van Duzee)

50. Basal segment of hind tarsi not more than 1½ times as long as distal; fore tarsi with basal segment subequal to or shorter than distal; width across base of pronotum greater than width across eyes.....51

Basal segment of hind tarsi twice as long as distal; fore tarsi with basal segment distinctly longer than distal; width of pronotum across base equal to or less than width across eyes.....52

51. Abdomen elongate, its maximum width less than one-half its mesal length; small mesal sclerotized plate present on tergum 8, its width subequal to that of the posterior scent-gland plate; distance between openings of posterior scent gland one-half that between openings of anterior scent gland; eyes not in contact with pronotum.....**Paromius** Fieber
P. longulus (Dallas)

Abdomen ovoid, its width more than one-half its length; usually without a sclerotized plate on tergum 8, such plate if present much smaller than posterior abdominal scent-gland plate; distance between openings of posterior scent gland more than one-half that between openings of anterior gland; eyes often in contact with pronotum.....**Pachybrachius** Hahn
P. basalis (Dallas), *P. servillei* (Guérin), *P. bilobatus* (Say), *P. albocinctus* Barber

52. Antennal segment 1 one-half as long as interocular width of head, barely surpassing tylus; juga not carinate along lower margin; width across eyes greater than length of pronotum (1.10: 0.85).....**Sphaerobius** Uhler
S. insignis Uhler

Antennal segment 1 longer than interocular width of head, surpassing tylus by half its length; juga carinate along lower margin; width across eyes less than length of pronotum.....53

53. Pronotum wider than long, concolorous, its anterior lobe not swollen dorsally; spiracle of abdominal segment 2 definitely lateral on connexivum; abdominal coloration reddish.....**Pseudocnemodus** Barber
P. canadensis (Provancher)

Pronotum longer than wide, its dark-colored anterior lobe swollen dorsally and contrasting strongly with the light-colored posterior lobe; spiracle of abdominal segment 2 definitely dorsal; abdominal coloration yellowish.....**Cnemodus** Herrich-Schaeffer
C. mavortius (Say)

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Morphology and Phylogeny of the Reduvioidea (Hemiptera: Heteroptera). Part II. Wing Venation[1]

NORMAN T. DAVIS

University of Connecticut, Storrs

ABSTRACT

Evidences of the identity of the veins of the cubital-anal field of the hemipterous wing are given. In the fore wing of auchenorrhynchous Homoptera these veins are: Cu_1 (anterior to the clavus); Cu_2 (closely associated with the claval furrow); Pcu, 1st A, and 2d A (in the clavus). In Heteroptera Cu_2 is absent, and the clavus contains only Pcu and 1st A. There is no anal lobe in either suborder, the clavus representing the postcubital region of the fore wing. In the hind wing of Auchenorrhyncha the veins of the cubital-anal field are the same as in the fore wing; a cubital furrow lies just behind Cu_2, and the anal fold lies just behind 1st A. In Heteroptera this region of the hind wing is similar, except that Cu_2 is absent, and the cubital furrow often is bifid and may contain secondary veins between its branches. In both Auchenorrhyncha and Heteroptera the anal lobe of the hind wing usually is well developed, and the jugal lobe is always absent. In the Cimicomorpha the hind-wing venation of the Miridae, Nabidae, Microphysidae, Anthocoridae, Joppeicidae, Thaumastocoridae, and Velocipedidae is of the same basic type, characterized particularly by the absence of Sc and by having a Y- or V-shaped pattern of Pcu and 1st A. The tingids resemble this group, but have a distinct Sc. The nabids and microphysids seem exceptional in sometimes having R and M separated distally, as in the Pentatomomorpha. The reduviid venation is distinct from that of the other Cimicomorpha, and is best characterized by a narrow postcubital sector containing subparallel Pcu and 1st A veins. Venation is useful in distinguishing subfamilies of the Nabidae, Anthocoridae, and Reduviidae; in the Reduviidae it serves in characterizing three major groups of subfamilies.

The pattern of the metathoracic wing venation of several groups of the Heteroptera has been found by various authors to have characters useful in showing relationships particularly at the family and subfamily level (Slater and Hurlbutt, 1957; Leston, 1953a, b; Usinger, 1943; Drake and Davis, 1958). This study was therefore undertaken to determine the value in this regard of the hind wing venation of the reduvioids. In the course of the study it was found that the identity of some of the veins of the hind wing of Heteroptera was poorly established and so consideration was given to this matter as well.

The naming of the wing veins of Heteroptera had its inception in a study by Comstock and Needham (1898). These authors found that there are six principal tracheae and corresponding veins in each wing and designated these as the costa, subcosta, radius, media, and first anal vein. Later Handlirsch (1908) presented evidence indicating that the costa is absent in the Heteroptera and he therefore renamed the veins, the costa becoming the subcosta, the subcosta becoming the radius, and so on.

In his extensive study of the venation of the Heteroptera this view of the loss of the costa was adopted by Tanaka (1926), who also contributed significantly to the general recognition that the so-called first anal vein of the Comstock-Needham system is in many insects actually the second branch of the cubitus. In the same year Hoke (1926) published an extensive study of the venation of the Heteroptera but followed Comstock and Needham in designating the first vein as the costa. Since the view that the costa is absent in the Heteroptera has generally prevailed, Hoke's work has not been as widely accepted and influential as that of Tanaka.

Recently Leston (1953a,b) has reinterpreted some of the veins identified by Tanaka. The basis for this reinterpretation is as follows: Tanaka had described a bifurcating furrow behind the cubitus and termed it the anal furrow. He noted that it contained between its branches certain indistinct veins which he termed the secondary veins. This region is followed by two well developed veins which Tanaka designated as the 1st A and 2nd A_1. Posterior to the 2nd A_1 there is what Tanaka designated as the subanal fold and this fold sets off what he termed the subanal lobe which contains a vein designated as the 2nd A_2. Leston, following the general scheme of wing venation of Snodgrass (1935), concluded that the so-called anal furrow is the vannal (anal) fold of the wings of other insects, that the sector of the wing behind it is the vannal (anal) lobe, that the so-called subanal fold is the jugal fold, and that this fold sets off the jugal lobe. The names of the veins were accordingly changed, the secondary veins being renamed the intervannal veins, followed by the 1st and 2nd vannals, and these in turn followed by the jugal vein.

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The changes made by Leston seemingly provide a terminology that is consistent and uniform with that of the wings of other insects, and they have been adopted by a number of hemipterists. Unfortunately, with further study several discrepancies appear which cast considerable doubt upon Leston's interpretation. First of all, one would not expect to find a well developed jugal lobe on a wing so reduced as that of the Heteroptera. Generally the jugal region is considered to be a recent and secondary development of the insect wing. In most insects on which it occurs it is a small, inconspicuous lobe and in the auchenorrhynchous Homoptera, which clearly have the most generalized wings of the Hemiptera, the jugal region is absent. The heteropteran hind wing, through a process of reduction, has probably been derived from a wing very much like that of the Auchenorrhyncha, and it seems quite unlikely that while the heteropteran wing was undergoing reduction the jugal region would at the same time persist or become more prominent.

A study of the flexing mechanism indicates that the posterior lobe of the hind wing of Hemiptera is, in fact, the anal, rather than the jugal lobe. In neopterous insects generally, the anal lobe constitutes that portion on the wing which is turned under when the wing is folded over the back. The third axillary sclerite, (fig. 6, Ax3) which is the principal skeletal element in the flexing mechanism, lies at the base of the anal lobe (AL) and the anal veins arise from it (1A, 2A). The anal fold extends from the anterior edge of the third axillary sclerite (AF) and generally lies just in front of the first anal vein; but, according to Snodgrass (1935), it varies somewhat in position, running anterior to the postcubitus in the Plecoptera and behind the first anal vein in the cicada. Since the anal lobe turns under when the wing is flexed, the anal fold is always convex.

The posterior lobe of the hind wing of heteropterans conforms essentially with these general characteristics of the anal lobe of insects (fig. 17, AL). However, that portion of the wing designated by Leston as the vannal (anal) lobe (PcuS) lies with its base anterior to the third axillary sclerite and does not fold when the wing is flexed; the so-called fold on its anterior margin is not a fold, but a furrow, and is concave rather than convex. Such furrows are not uncommon in the medial and cubital regions of the wings of insects.

Since the current interpretation of the hind-wing venation of the Hemiptera is apparently inadequate in certain respects, the identity of the veins has been reinvestigated and new evidences and conclusions are presented below.

VENATION OF AUCHENORRHYNCHOUS HOMOPTERA

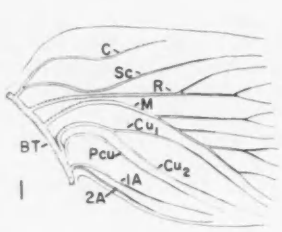
The identity of the veins of the fore and hind wing of the Heteroptera may be more accurately determined through a comparative study of the venation of the auchenorrhynchous Homoptera. Of this group the Fulgoroidea appear to have rather primitive venation and serve well as a model of the prototype venation of the Order.

The identity of the wing veins of the Fulgoroidea was established by Metcalf (1913), who followed the Comstock-Needham designations; the venation has since been clarified with regard to the identity of the costa and cubital veins by Fennah (1944). The salient features of the tracheation of the fore wing, as shown by Fennah, are as follows: In the fore-wing pad there are six tracheal trunks arising from the basal trachea (fig. 1, BT). The first of these divides proximally into the tracheae of the costa (C) and subcosta (Sc) and is followed by the two tracheae of the radius (R) and media (M). The fourth trunk divides deeply into the tracheae of the 1st cubitus (Cu_1) and 2d cubitus (C_2). From near the base of the cubital trachea arises the postcubital trachea (Pcu), which is followed by the two-branched anal trachea (1A, 2A). In the adult fore wing Sc, R, and M proximally form a common vein, then separate and give rise to several branches (fig. 2). Vein Cu_1 divides deeply into two branches and meets Cu_2 at its basal connection. The clavus is set off by a distinct furrow (ClFr) which lies just behind Cu_2, and in addition to Cu_2 the clavus contains Pcu and the two anal veins.

The basic pattern of tracheation of the hind-wing pad is essentially the same as that of the fore wing (fig. 3). A study of this tracheation and the hind-wing venation of other Homoptera indicates that Fennah has incorrectly identified the Cu_{1b} as Cu_2 and consequently the succeeding veins are wrongly designated. The Cu_1 trachea and vein divide about midway in the wing just as the Cu vein does in the fore wing, giving rise to Cu_{1a} and Cu_{1b} (figs. 3, 4). The Cu_2 trachea and vein arise from the base of Cu_1 and, as in the fore wing, a furrow is associated with this vein (CuFr). This cubital furrow is equivalent to the claval furrow of the fore wing and, likewise, lies just behind Cu_2. The next vein may be identified as the postcubitus (Pcu) by the fact that its trachea arises from the basal trachea between the cubital and anal trunks and by the fact that basally it is associated with both the second and third axillary sclerites. The first anal vein is joined to the anterior edge of the third axillary sclerite and the anal fold lies behind this vein. The second anal vein lies in the anal lobe.

A comparison of the fore and hind wings of fulgoroids shows that the fore wing lacks an anal lobe and that the clavus is, more or less, equivalent to that portion of the hind wing between the cubital furrow and the anal fold. The base of the clavus is attached to the anterior apex of the third axillary sclerite and through this point of attachment the fore wing is pulled back into the folded position by the third axillary.

The wing venation of the Cicadidae has been thoroughly reviewed by Myers (1928), who pointed out that the vein identified by Comstock and Needham as the 1st A is actually Cu_2. This vein arises from



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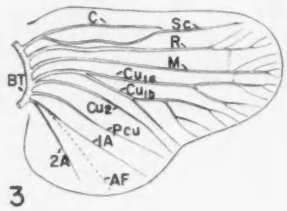

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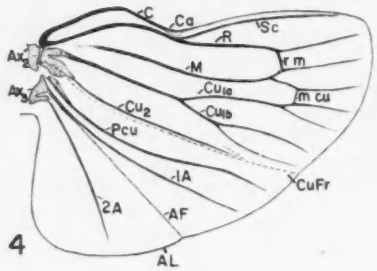

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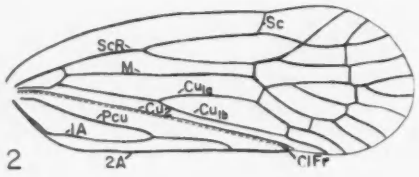

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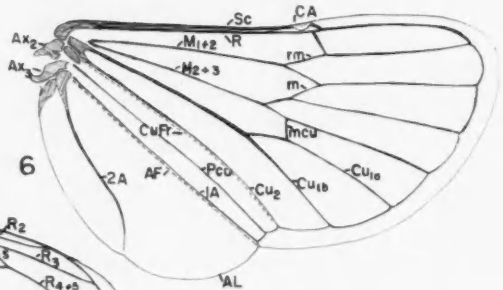

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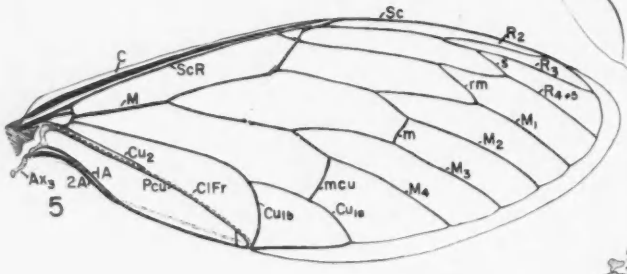

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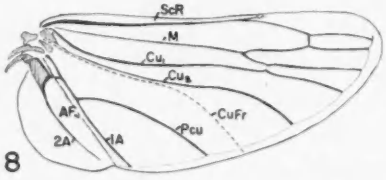

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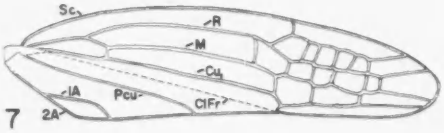

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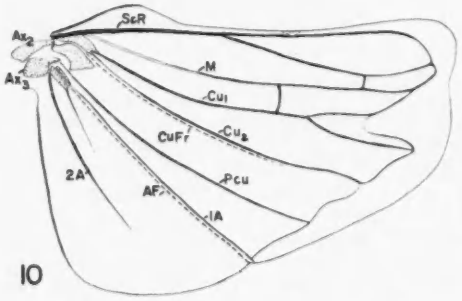

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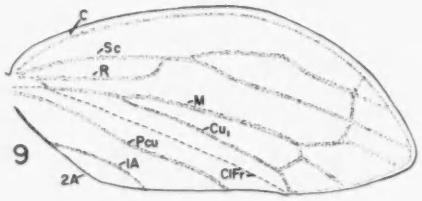

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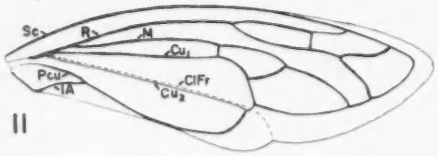

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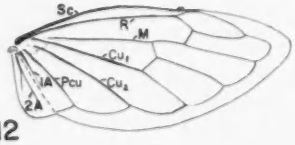

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the base of Cu_1 and proximally is just in front of the claval furrow (fig. 5). However, about midway in its course it crosses the furrow and fuses with a vein lying immediately behind the claval furrow. This latter vein heretofore has usually been designated as the 1st A but it is identical to the postcubitus of the fulgoroids and should be termed such. The remaining veins in the clavus should be designated as 1st and 2d A. The clavus is commonly considered to be homologous to the anal lobe but, as noted above with regard to the fulgoroids, this interpretation is incorrect since the anal area of the fore wing has been eliminated.

In the cicada hind wing Myers has also shown the proper designation of the Cu_2 which extends for its full length just in front of the cubital furrow (fig. 6). Snodgrass (1935) has indicated that the next vein is the postcubitus and properly labeled the remaining anal veins. As in the fulgoroids the anal fold lies just behind the 1st A.

The identity of the wing veins of the Cicadellidae were determined by Metcalf (1913), those of the Cercopidae by Metcalf (1917), and those of the Membracidae by Funkhauser (1913). Since the Cu_2 and Pcu were not recognized at the time of those studies, the cubital and anal veins are commonly incorrectly designated in the literature. In the fore wing of the Cicadellidae the Cu_2 borders the cubital furrow posteriorly but, since it is weakly developed and inconspicuous, it is frequently indistinguishable (fig. 7). However, the presence of this vein is indicated by a trachea clearly visible in recently molted adults. As in the preceding families the remaining veins of the clavus should be designated respectively as the Pcu, 1st A and 2d A.

In the cicadellid hind wing Cu_2 lies in front of the cubital furrow, and behind the furrow is found the characteristic Y-shaped pattern of venation formed by veins which should be designated as the Pcu and 1st A (fig. 8). Proximally the 1st A originates from the third axillary sclerite behind the anal fold, but a short distance out it passes over the fold where it joins the Pcu forming a common stem before the two veins diverge distally. The anal lobe contains a single vein, the 2d A.

The fore wing of the Cercopidae is generally rather coriaceous throughout and consequently the veins are indistinct (fig. 9). In most cases the Cu_2 cannot be distinguished but, as in the Cicadellidae, the Cu_2 trachea may be found bordering the cubital furrow posteriorly. The Pcu, 1st A, and 2d A, however, can generally be distinguished. As may be seen in figure 10, the cubital and anal venation as well as the cubital furrow and anal fold of the hind wing of cercopids are in essentially the same position as indicated in the families already considered.

The wing venation of the Membracidae is the most highly modified of the auchenorrhynchous Homoptera but the major veins can be identified (fig. 11). Compared to the other veins in the fore wing, Cu_2 is rather weak and inconspicuous. The cubital furrow lies along its anterior edge but is also inconspicuous, and the clavus, therefore, is poorly differentiated. The Pcu is independent proximally but curves back distally to join the 1st A, and the 2d A runs closely parallel to the latter. Funkhouser has shown there are trachea which correspond to these veins in the cubital-anal region of the fore wing.

The hind wing is characterized by the great reduction of the anal lobe and the loss of 2d A (fig. 12). The Pcu and 1st A form a Y-shaped pattern similar to that found in the cercopids. The Cu_2 is distinct and lies just in front of a poorly developed cubital furrow.

From the foregoing descriptions, the positions of the cubital, postcubital, and anal veins, as well as the cubital furrow and anal fold, are seen to be very consistent in the Auchenorrhyncha. In contrast the pattern of the costal, radial, and medial veins of the fore wings show considerable differences between families. The fore-wing venation of the Cicadellidae (fig. 7), in which Sc lies near the costal margin and R and M are confluent for a considerable distance from the base, is quite similar in these respects to that found in most Heteroptera. However, it remains to be seen if this similarity is of any particular significance. In both the fore and hind wing of the Auchenorrhyncha the costal trachea and vein are considerably reduced or entirely absent. This condition appears an antecedent of the complete loss of the costa in all Heteroptera.

The basic venation of the auchenorrhynchous hind wing is rather similar in the several families; the principal exception is found in the Cicadidae, in which the media divides into two trunks very deep in the wing (fig. 6). In all of the families the Sc and R are confluent for most of their length and lie near the costal margin, while M runs separately and is poorly developed proximally. Also in each family there are consistently a r-m and an m-cu cross-vein.

One final feature of the wings of the Auchenorrhyncha to be mentioned is the mechanism for locking the fore and hind wing together. It consists of a recurved, tooth-like lobe on the costal margin of the hind wing (fig. 6, CA) which, when the wings are spread for flight, catches in the turned-under

FIG. 1.—Tracheae of fore-wing pad of *Poekilloptera phalaenoides* (L.) (Fulgoroidea), after Fennah 1944. FIG. 2.—Fore wing of *Cixius basalis* V. D. (Fulgoroidea). FIG. 3.—Tracheae of hind-wing pad of *Poekilloptera phalaenoides*, after Fennah 1944. FIG. 4.—Hind wing of *Ormenis septentrionalis* (Spinola) (Fulgoroidea). FIG. 5.—Fore wing of *Magicicada septendecim* (L.) (Cicadidae). FIG. 6.—Hind wing of *Magicicada septendecim*. FIG. 7.—Fore wing of *Draeculacephala mollipes* (Say) (Cicadellidae). FIG. 8.—Hind wing of *Draeculacephala mollipes*. FIG. 9.—Fore wing of *Lepyronia quadrangularis* (Say) (Cercopidae). FIG. 10.—Hind wing of *Lepyronia quadrangularis*. FIG. 11.—Fore wing of *Ceresa bubalus* (Fabr.) (Membracidae). FIG. 12.—Hind wing of *Ceresa bubalus*.

hind margin of the clavus (fig. 5). This arrangement is in contrast to that of the Heteroptera, in which a spur near the apex of the clavus catches in a groove (fig. 17, CA) along the costal edge of the hind wing. These coupling devices have been described in considerable detail by Teodoro (1924a,b,c).

VENATION OF HETEROPTERA

A review of the wing tracheation of the Heteroptera given in the literature as well as a study of representatives of several families of Heteroptera made in connection with the present paper shows that, as in the Auchenorrhyncha, there are six principal tracheae arising from the basal trachea in both the fore and hind wing. Originating anterior to the others is a single, unbranched trachea corresponding to the C-Sc stem of the Auchenorrhyncha but lacking the reduced costal branch of the latter (figs. 13, 14, Sc). Next there arise very close together (Hydrocorisae), or from a short, common basal stem (Geocorisae), the radial and medial tracheae (R, M). The last three tracheae arise together posteriorly from the basal trachea and are clearly the tracheae of the cubital-anal field (Cu, Pcu, and 1A). The first of these tracheae arises independently or from a common stem and is the cubital trachea. In the fore wing this trachea commonly divides into a small anterior branch and a larger posterior branch which becomes coincident with the cubital vein (fig. 13, Cu). Tanaka (1926) suggested that the anterior branch may represent the trachea of Cu_1, which has become obsolete in Heteroptera, and that the cubital vein of Heteroptera is Cu_2. One difficulty with this theory is that in the Auchenorrhyncha Cu_2, as we have seen, usually lies behind the claval furrow while in the Heteroptera the trachea and vein in question always lie anterior to it (fig. 15, Cu). An alternative and perhaps more suitable explanation is that these two tracheae represent Cu_{1a} and Cu_{1b}, and that Cu_{1a} has become obsolete.

The next two tracheae in the fore wing correspond to the vein in the clavus. However, it is necessary to determine which of the four veins present in the auchenorrhynchous clavus these two tracheae represent. Since their origin on the basal trachea is highly modified, no evidence as to the identity of these claval veins can be gained from this feature. We may note, however, that the Cu_2 and 2d A frequently undergo great reduction in the Auchenorrhyncha and consequently conclude that these veins have probably been lost in the Heteroptera, leaving only the Pcu and 1st A. Thus the principal veins of the heteropteran hemelytra are Sc, R, M and Cu extending through the corium, and Pcu + 1st A in the clavus (fig. 15).

In the hind wing the last two tracheae (figs. 14, 16) coincide with the two veins lying immediately anterior to the anal fold and thus correspond in position to the Pcu and 1st A of the Auchenorrhyncha. The single vein in the anal lobe (fig. 16, 2A) would thus be the 2d A; it generally lacks a trachea and in the teneral adult one can see that the tissue associated with it is supplied by minute tracheae extending posteriorly from the 1st A trachea. However, in certain pentatomids Tanaka (1926) found that this vein is supplied with a small, independent trachea arising from near the base of the 1st A trachea, and this observation has been confirmed in the present study. Even if no instance were known of this vein being preceded in development by an independent trachea, it would be an abuse of the theory of recapitulation to conclude that it is therefore not a true vein and not homologous to the 2d A of the Auchenorrhyncha. Since the vein in the anal lobe has the same relationship to the third axillary sclerite (fig. 17, 2A, Ax3) as the corresponding vein in the Auchenorrhyncha, it would be illogical to propose that the 2d A has been lost and that a jugal vein developed in its place.

As in the fore wing, the Cu_2 trachea and vein have not been found in the hind wing. The cubital furrow, normally associated with this vein in the Auchenorrhyncha, is present in the heteropterous hind wing but it is usually forked (fig. 17, CuFr). The anterior branch appears to be a secondary development and the posterior furrow appears to correspond to the original one since it is usually more distinct. The area of the wing delineated by the branches of the cubital furrow will be designated here as the cubital sector (CuS) and the area of the wing between the posterior cubital furrow (CuFr) and the anal fold will be designated as the postcubital sector (PcuS).

The identity of the veinlike structures often found in the cubital sector remains to be determined. The fact that they lack independent tracheae cannot be taken as proof that they are not homologous to certain veins of other insects for the same reasons indicated with regard to the atracheate 2d A vein. However, the lack of independent tracheae does make it difficult to identify them. Possibly, in forms such as the Miridae which have a single vein in this area (fig. 22, SV), this vein represents the remnant of Cu_2, but since there more commonly are two veins in the cubital sector (fig. 23, SV), one or both may be spurious. For the present it seems best to designate these as the secondary veins, following the terminology originally proposed by Tanaka (1926).

The pattern of venation of Sc, R, M, and Cu in the hind wing is, in general, characteristic for the three major divisions of the Heteroptera. The Saldidae, however, are different from all other Heteroptera in that they have both a distinct r-m and an m-cu cross-vein and thus resemble the Auchenorrhyncha in this respect (fig. 17). In most of the Hydrocorisae M distally joins Cu and thence curves forward to meet R (fig. 18). The Sc is usually indistinguishable and Cu is very often obsolete beyond its junction with M. The Notonectidae (fig. 20) and Gelastocoridae differ from the other Hydrocorisae; in these families M does not meet Cu but is joined to it by a cross vein instead.

In the Amphibicorisae the proximal portion of M (viz., the hamus) is absent and the remainder of M forms a vein extending diagonally between R and Cu (fig. 19). The Sc is indistinguishable.

As Leston et al. (1954) have pointed out, two general types of patterns of hind-wing venation may be distinguished in the Geocorisae and these differences constitute one of the characterizing features of the Cimicomorpha and the Pentatomomorpha. In the Pentatomomorpha, according to these authors, the Sc is obsolete and the hamus may be distinct or absent (fig. 23). Usually a portion of M is broadly joined to Cu and thence passes anteriorly to join R and then diverges from it distally. The m-cu and the r-m crossveins are usually absent but never are they both present.

In the Cimicomorpha the Sc and hamus vary from distinct to absent (figs. 25, 32). The M may be either fused with, or joined to the Cu by a cross vein; it then runs anteriorly to join R with which it is almost always from thereon coincident to the apex.

HIND WING VENATION OF THE CIMICOMORPHA

Miridae.—The metathoracic wing venation of this family is very consistent and there appears to be no significant difference between subfamilies (fig. 22). The venation may be characterized as follows: Sc indistinct and marginal; hamus lacking; M distinguishable only as a diagonal vein connecting R and Cu; only one secondary vein present; Pcu and 1st A joined proximally and strongly divergent distally, forming a Y-shaped pattern; 2d A often obsolete.

The following material was examined: *Megalocerocа reticornis* (Geoff.), *Lygus* (*Exolygus*) *linearis* (P. de B.), *Adelphocoris rapidus* (Say), and *Poecilocapsus lineatus* (Fabr.) (Mirinae); *Orthocephalus mutabilis* (Fall.) and *Labops hirtus* Knight (Orthotylinae); *Plagiognathus politus* Uhler and *Dicyphus agilis* Uhler (Phylinae); *Deraeocoris borealis* Van Duzee (Deraeocorinae); *Corticoris pulchellus* (Heid.) (Isometopinae).

Tingidae.—Except for modifications associated with the brachypterous condition common in this family, the metathoracic wing venation is quite consistent even between the subfamilies (fig. 21). The venation may be characterized as follows: Sc usually distinct, marginal, and becoming submarginal distally; hamus lacking, M distinguishable only as a diagonal vein connecting R and Cu; two secondary veins present; Pcu and 1st A joined proximally and distally divergent, forming a Y-shaped pattern; anal lobe and 2d A always absent except in some Cantacaderinae.

The following material was examined. *Paracopium* sp., *Derephysia foliacea* (Fallén), *Leptodictya ochropa* (Stål) *Agramma atricapilla* (Spin.), *Corythucha bulbosa* Osborn and Drake, *Dulinius conchatus* Dist., and *Tingis cardui* (Linn.) (Tinginae); *Cantacader tener* Bergroth, and *Stenocader* sp. (Cantacaderinae).

Anthocoridae.—In this family the hind wing venation is rather consistent, except for the development of the hamus which is different in the three subfamilies. In the Anthocorinae (fig. 24) the hamus joins the cubitus directly, while in the Lyctocorinae it is joined to the cubitus by the m-cu cross vein, and in the Duforiellinae the hamus is absent. These differences are used in distinguishing the subfamilies (China and Miller 1959) but may not always be suitable for the Lyctocorinae since in *Lasiochilus pallidulus* Reuter, for example, the hamus is obsolete (fig. 25).

The hind wing may otherwise be characterized as follows: Sc indistinct and marginal, the cubital sector containing only the posterior secondary vein; the Pcu and 1st A only moderately divergent distally and the 1st A often reduced in length, 2d A absent.

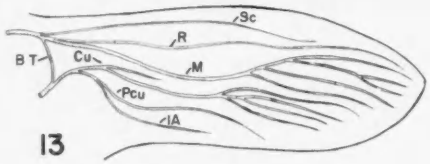
The foregoing characterization is based on an examination of *Anthocoris borealis* Dallas and *Orius insidiosus* (Say) (Anthocorinae); *Lasiochilus pallidulus* Reuter (Lyctocorinae), and on various descriptions given in the literature.

Joppeicidae. In the single member of this family the hind wing may be characterized as follows: Sc indistinct and marginal; hamus lacking; M distinguishable only as a diagonal vein between R and Cu; cubital furrow not forked; secondary veins absent; Pcu well developed but 1st A vestigal and 2d A absent (fig. 27). The wing of *Joppeicus paradoxus* Puton has been studied in the present work and by China (1955) previously.

Thaumastocoridae.—In this family the hind wing may be characterized as follows: Sc indistinct and marginal, hamus lacking, M distinguishable only as a diagonal vein between R and Cu, cubital furrow not forked, secondary veins absent, Pcu well developed but 1st and 2d A absent (fig. 26). This characterization is based on a study of *Xylastodoris luteolus* Barber (Xylastodorinae) and the figure of the hind wing of *Baclozygum depressum* Bergroth (Thaumastocorinae) given by Drake and Slater (1957).

Microphysidae.—The hind wing venation of this family is known from the figure of the wing of *Mallochiola gagates* (McAtee and Malloch) (fig. 28) given by McAtee and Malloch (1924); it may be characterized as follows: Sc indistinct or absent; hamus absent; M distinguishable as a diagonal cross between R and Cu and distally branching from R; secondary veins absent and cubital furrow not forked, Pcu and 1st A moderately divergent; 1st A reduced and anal lobe apparently lacking.

Velocipedidae.—The hind wing venation of this monogeneric family is represented here by *Scotomedes alienus* (Distant) and may be characterized as follows: Sc marginal; hamus present; M narrowly joined to Cu; secondary veins lacking; Pcu and 1st A joined basally and widely divergent distally; 2d A absent and anal lobe reduced (fig. 29).



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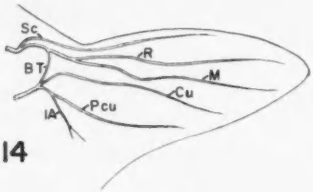

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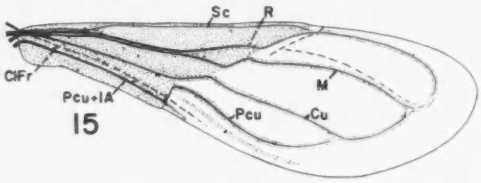

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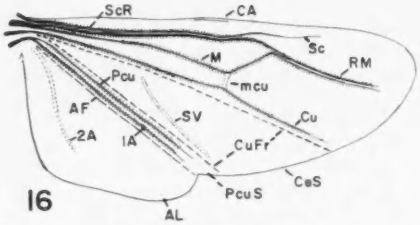

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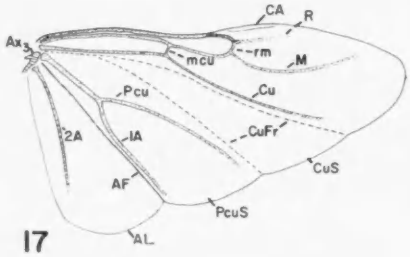

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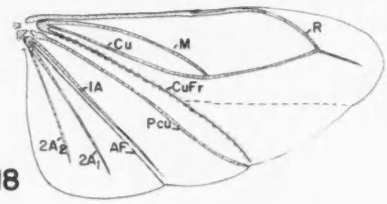

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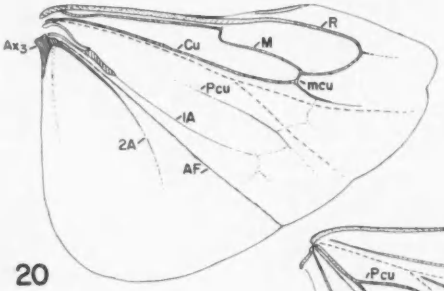

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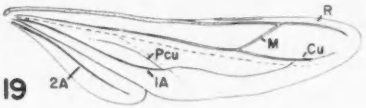

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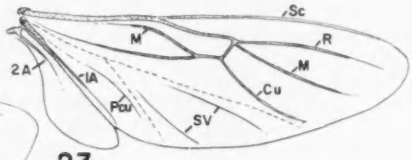

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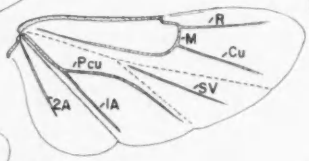

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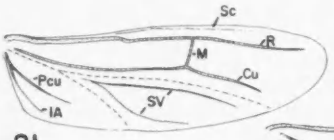

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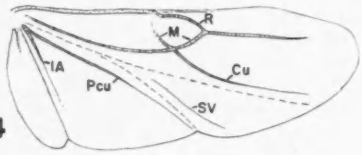

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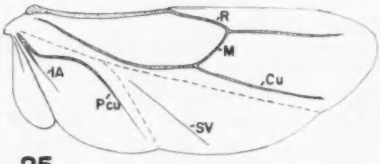

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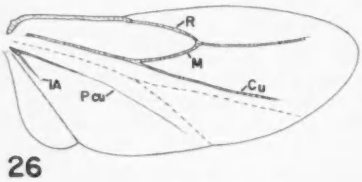

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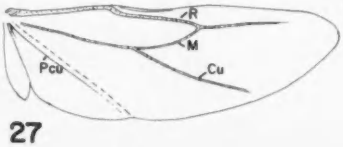

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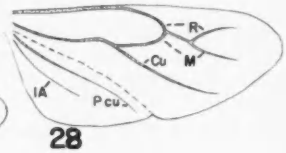

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Nabidae.—The hind wing venation varies from one subfamily to the next and therefore the venation of this family is not easily characterized. In general it is as follows: Sc indistinct and marginal; hamus present or absent; M and R often distally divergent; secondary veins vary from two to one to none; Pcu and 1st A fused basally and strongly divergent distally; 2d A usually absent. In the Carthasinae (fig. 30) the hamus is absent, M remains coincident with R distally, and both secondary veins are present. In the Arachnocorinae (fig. 31) the hamus again is absent, but M diverges from R distally. The cubital furrow is not forked, the secondary veins are absent, the Pcu and 1st A are obsolete, and the anal lobe is lacking. In the Prostemminae (fig. 32) the hamus is present, M joins Cu directly and does not diverge from R distally, and the cubital furrow is forked but the secondary veins are lacking. In the Nabinae (fig. 33) the hamus is present, M is joined to Cu by the m-cu cross-vein and diverges distally from R, and only the posterior secondary vein is present.

The foregoing characterizations are based on an examination of the wings of *Arachnocoris albomaculatus* Scott (Arachnocorinae), *Carthasus decoratus* (Uhler) (Carthasinae), *Pagasa fusca* Stein (Prostemminae), and several species of *Nabis* (Nabinae).

Pachynomidae. As a representative of this small family, *Punctius alutaceus* Stål has been studied and its hind wing (fig. 34) may be characterized as follows: Sc feebly developed and marginal; hamus absent, M distinguishable only as a transverse vein between R and Cu; secondary veins feebly developed; Pcu and 1st A poorly developed but apparently fused basally for about half their length and then diverging; anal lobe and 2d A well developed.

Reduviidae.—In this relatively large and diverse group the hind wing venation varies considerably, but these variations for the most part do not reflect subfamily differences (figs. 35-63). The development of the Sc varies from indistinguishable to distinct, and may extend along the costal margin or lie below it. The hamus may be absent, short, or well developed, and when present may join Cu, but more commonly it extends from the m-cu cross-vein. Two secondary veins are usually present, and the cubital furrow lacks a common basal stem so that the cubital sector extends nearly to the wing base. The Pcu and 1st A may be fused or contiguous basally but, unlike these veins in other cimicomorphs, they are subparallel or diverge relatively little and often converge distally. The postcubital sector, which contains these veins, is correspondingly narrow. The 2d A and anal lobe are usually well developed.

Since the reduviid subfamilies are so numerous and there is relatively little difference in the hind wing venation of many of them, it is more convenient to discuss their venation on the basis of groups of apparently related subfamilies. However, no formal taxonomic status is intended for the subfamily complexes to be described below and it is anticipated that additional evidences indicating the subfamily relationships will be discussed more fully in a future publication.

Davis (1957) and Carayon et al (1958) have noted that the Elasmodeminae, Holoptilinae and phymatines constitute a group of related forms, and the latter authors have placed the phymatines as a subfamily of the Reduviidae.[2]

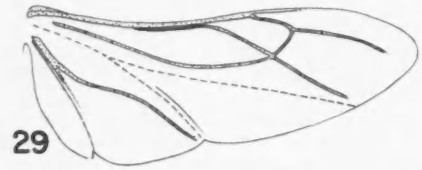
These subfamilies will be referred to here as the Phymatine Complex. The Phimophorinae, Mendanocorinae, and Centrocneminae are probably also related to this complex.

The hind wing of members of the Phymatine Complex may be characterized by the fact that Sc generally arises from R where the latter leaves the costal margin of the wing, and Sc thence extends along the costal margin or just below it (figs. 35-42). This complex is further characterized by the reduction or loss of the hamus in some of its members. The hamus is absent in the Elasmodeminae (fig. 36), Holoptilinae (fig. 37), Phimophorinae (fig. 38), and the genus *Carcinocoris*[3] of the Phymatinae (fig. 39). The remainder of the Phymatinae (viz. *Phymata*, fig. 35; *Macrocephalus*, fig. 41; and Themonocorini, fig. 40) have a reduced hamus but differ from most other reduviids in lacking the m-cu cross-vein, as

[2] This reduced status of the phymatines has not been accepted by all authorities (see China and Miller 1959), but since there has been no refutation as yet of the details of the argument presented by Carayon et al. the phymatines are treated here as a subfamily of the Reduviidae.

[3] In reducing the phymatines to the rank of subfamily, Carayon et al. (1958) in effect suppressed the three subfamilies (Phymatinae, Carcinocorinae, and Macrocephalinae) which formerly constituted the group as a family. However, the change of status apparently was based only on a study of members of the subfamily Phymatinae *sensu latu*, and the question of the status of the former subfamilies Carcinocorinae and Macrocephalinae has not specifically been considered. The carcinocorines are distinct from other members of the tribe Phymatini in the form of the male genitalia (Davis 1959), in having chelate fore legs, and in lacking a hamus. Since these differences appear to be of the same magnitude as those between the Phymatini and the Themonocorini, consistency requires that tribal status be given to the Carcinocorini.

FIG. 13.—Tracheae of fore-wing pad of *Triatoma protracta* (Uhler) (Reduviidae). FIG. 14.—Tracheae of hind-wing pad of *Triatoma protracta*. FIG. 15.—Fore wing of *Triatoma protracta*, showing the course of the tracheae (black) in the wing veins. FIG. 16.—Hind wing of *Triatoma protracta*, showing the course of the tracheae (black) in the veins. FIGS. 17 to 28.—Hind wings of various Hemiptera, as follows. FIG. 17.—*Saldula interstitialis* (Say) (Saldidae). FIG. 18.—*Lethocerus americanus* (Leidy) (Belostomatidae). FIG. 19.—*Gerris marginatus* Say (Gerridae). FIG. 20.—*Notonecta undulata* Say (Notonectidae). FIG. 21.—*Cantacader quadricornis* (Lepeletier and Serville) (Tingidae). FIG. 22.—*Lygus lineolaris* (P. de B.) (Miridae). FIG. 23.—*Alydus curinus* Say (Alydidae). FIG. 24.—*Anthocoris borealis* Dallas (Anthocoridae; Anthocorinae). FIG. 25.—*Lyctocoris campestris* (Fabr.) (Anthocoridae; Lyctocorinae). FIG. 26.—*Xylastodoris luteolus* Barber (Thaumastocoridae). FIG. 27.—*Joppeicus paradoxus* Puton (Joppeicidae). FIG. 28.—*Mallochiola gagates* (McAtee and Malloch), after McAtee and Malloch 1924.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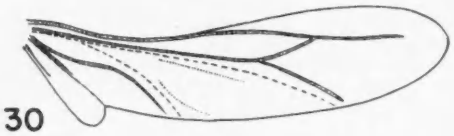
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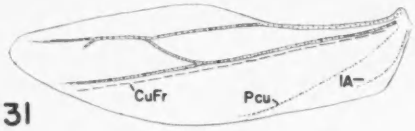

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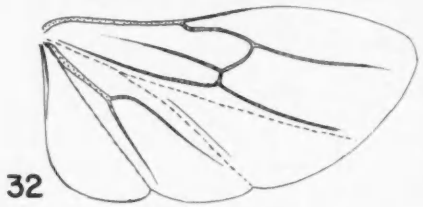
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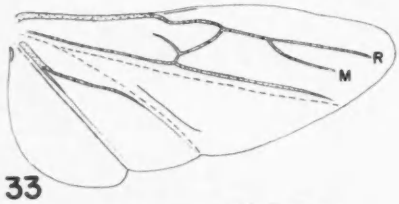

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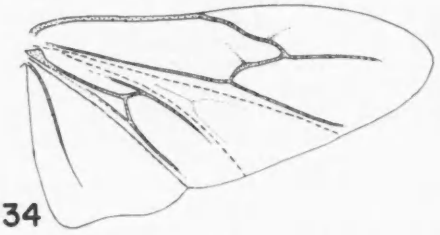
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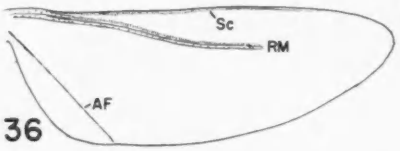

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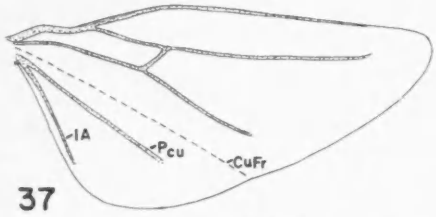

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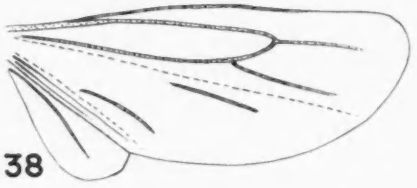
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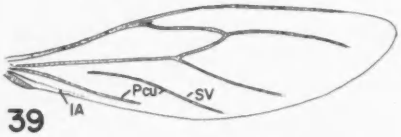

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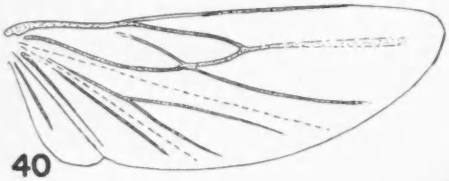
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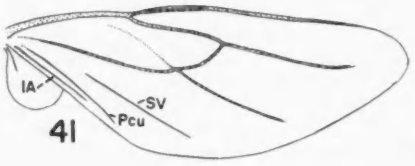

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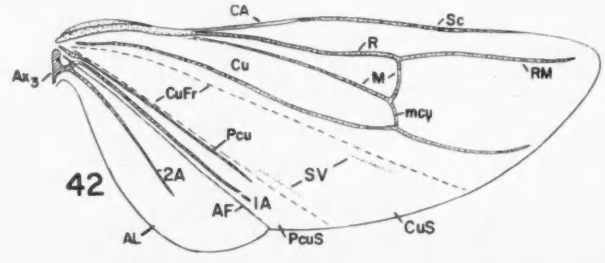

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a consequence of which their hamus arises directly from Cu. In the Centrocneminae (fig. 42) and Mendanocorinae (Miller 1956) the hamus is well developed and arises from the m-cu cross-vein. In most Phymatinae and in the Holoptilinae and Elasmodeminae the secondary veins are absent and the cubital furrow, if present, is not forked; in the Themonocorini of the Phymatinae, the Phimophorinae, and Centrocneminae the secondary veins and cubital furrow are developed normally. The venation of the Centrocneminae and Themonocorini appears to be the most generalized of this complex, while that of the Holoptilinae and most Phymatinae is somewhat reduced and that of the Elasmodeminae very reduced, consisting only of an obscure Sc and a heavy vein which perhaps consists of R and Cu.

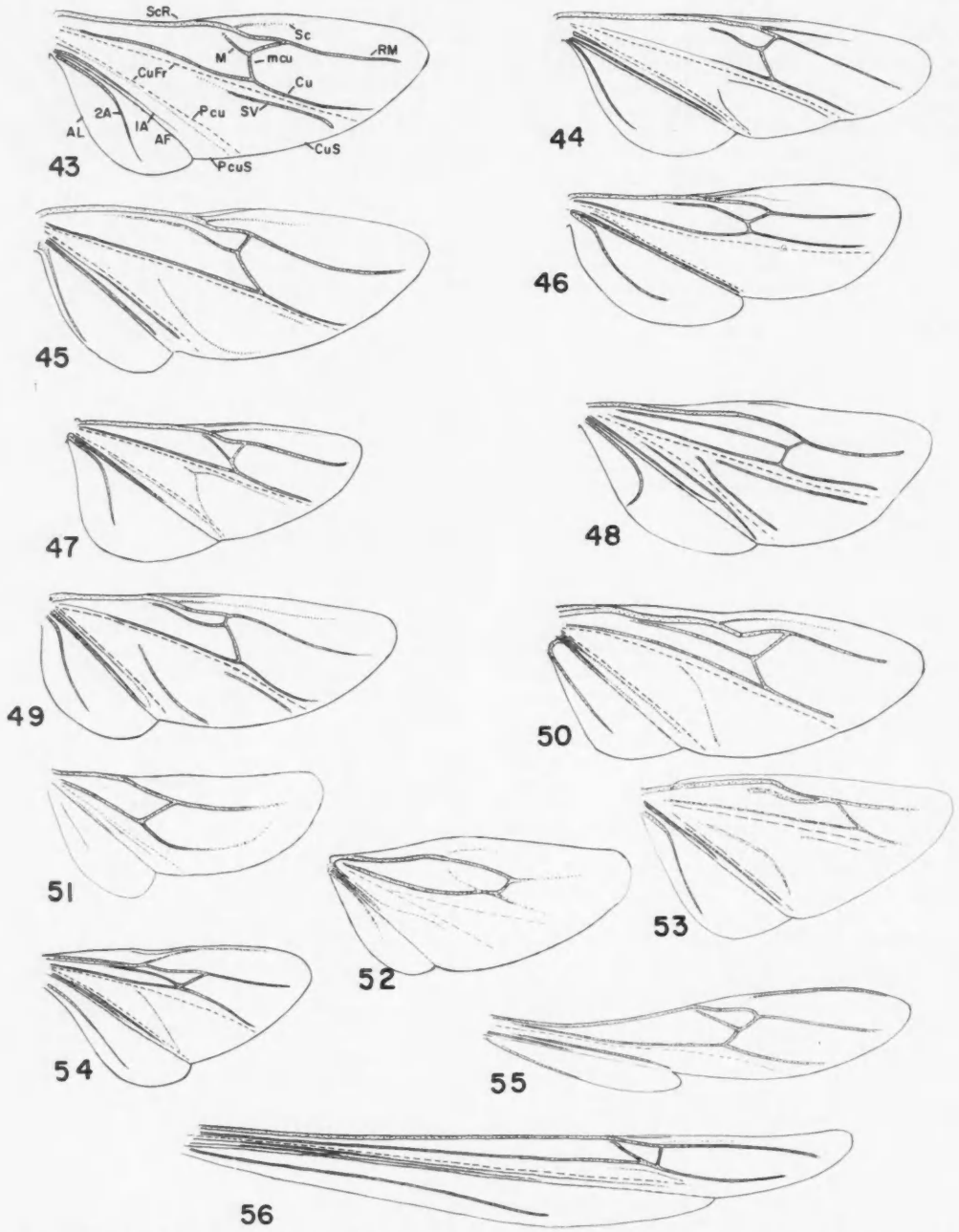
The foregoing characterization of the hind wing of the Phymatine Complex is based upon an examination of *Elasmodema erichsoni* Stål (Elasmodeminae); *Ptilocnemis femoratus* Horváth (Holoptilinae); *Macrocephalus tuberosus* Westwood, *Phymata fortificata* (Herrich-Schaeffer), *P. pennsylvanica* Handlirsch, *Carcinocoris castetsi* Handlirsch, and *Themonocoris kinkalanus* Carayon, Usinger, and Wygodzinsky (Phymatinae); *Phimophorus spissicornis* Bergroth (Phimophorinae); *Neocentrocnemis stali* (Reuter) (Centrocneminae); and of the illustration by Miller (1956) of the hind wing of *Mendanocoris browni* Miller (Mendanocorinae).

Members of the Phymatine Complex are, for the most part, diurnal predators that capture their prey by ambush rather than by active pursuit. On the other hand, there is a second group of reduviid subfamilies which, for the most part, are nocturnal and actively pursue their prey. Often they are ground dwellers and rapid runners. They are somewhat difficult to define as a group by morphological features, but predominantly they have a row of bristles forming a comb located basally on the anterior lateral surface of each hind coxa. As the coxa rotates the bristles rub against the serrated edge of the coxal cavity, and this movement causes them to bend and flick in a distinctive, wavelike fashion. These hind coxal combs probably serve to disseminate the secretion from the ventral metathoracic scent glands. They are best developed in the piratines, and therefore the group of subfamilies having this characteristic is termed here the Piratine Complex. In addition to the Piratinae the complex includes the Vesciinae, Salyavatinae, Cetherinae, Reduviinae, Triatominae, Stenopodinae, Chryxinae, Emesinae, Saicinae, and Sphaeridopinae.

The features of the hind wing in this group are somewhat variable and not clearly definable. Generally the point where Sc leaves R and its course from there on is, in contrast to that of the Phymatine Complex, well below the costal margin (figs. 43-54). The hamus in the subfamilies Piratinae (fig. 43), Vesciinae (fig. 54), Salyavatinae (fig. 44), and most Emesinae (fig. 56) is short, somewhat reduced, and extends obliquely toward ScR near which it terminates. On the other hand, the hamus in the Triatominae (fig. 16), Sphaeridopinae (fig. 45), Chryxinae (fig. 48), Reduviinae (fig. 49), and Stenopodinae (fig. 50) is generally rather straight, gradually approaches the ScR, and often extends nearly to the axillary region. In the Saicinae (fig. 46) and the Cetherinae (fig. 47) the hamus may assume both forms described above. The development of the secondary veins varies considerably even within some subfamilies. They are lacking in the Saicinae and most Emesinae; in the Stenopodinae and Triatominae the anterior secondary vein is often obsolete, and in the triatomine genus *Cavernicola* both veins are absent and the sector formed by the cubital furrow is quite narrow. In the Piratinae the posterior secondary vein is usually obsolete and in the Salyavatinae, Cetherinae, and Chryxinae the development of the secondary veins is normal. In most members of the Piratine Complex the postcubital sector is very narrow and the Pcu and 1st A are very close together.

Notable variations in venation occur within several subfamilies of the Piratine Complex; these differences may be useful in generic or tribal diagnosis in the Saicinae and Emesinae while in the Reduviinae they probably indicate that the subfamily still contains some aberrant forms. For example, in *Microlestria fusciollis* Stål (fig. 51) the hamus and secondary veins are absent and the wing rather resembles that of some of the Phymatine Complex. The hamus of *Velitra philippina* Stål (fig. 53) arises from R and a cross-vein extends from R to Cu; these features are unknown in any other reduviid. In contrast, the m-cu cross-vein is absent in *Durgana rubra* Stål (fig. 52) and in this species the hamus arises from Cu. The lack of the m-cu cross-vein is a character of some of the members of the Phymatine Complex but is also found in some of the Emesinae and in *Cethera musiva* (Germar) of the Cetherinae.

FIGS. 29 to 42.—Hind wings of various Cimicomorpha, as follows. FIG. 29.—*Scotomedes ater* Stal (Velocipedidae). FIG. 30.—*Carthasis decoratus* (Uhler) (Nabidae; Carthasinae). FIG. 31.—*Arachnocoris albomaculatus* Scott (Nabidae; Arachnocorinae). FIG. 32.—*Pagasa fusca* (Stein) (Nabidae; Prostemminae). FIG. 33.—*Nabis roseipennis* Reuter (Nabidae; Nabinae). FIG. 34.—*Punctius salutaceus* (Stal) (Pachynomidae). FIG. 35.—*Phymata fortificata* (Herrich-Schaeffer) (Reduviidae; Phymatinae). FIG. 36.—*Elasamodema erichsoni* Stal (Reduviidae; Elasmodeminae). FIG. 37.—*Ptilocnemus femoratus* Horváth (Reduviidae; Holoptilinae). FIG. 38.—*Phimophorus spissicornis* Bergroth (Reduviidae; Phimophorinae).). FIG. 39.—*Carcinocoris castetsi* Handlirsch (Reduviidae; Phymatinae). FIG. 40.—*Themonocoris kinkalanus* Carayon, Usinger, and Wygodzinsky (Reduviidae; Phymatinae). FIG. 41.—*Macrocephalus tuberosus* Westwood (Reduviidae; Phymatinae). FIG. 42.—*Neocentrocnemis stali* Reuter (Reduviidae; Centrocneminae).



FIGS. 43 to 56.—Hind wings of Reduviidae of various subfamilies, as follows. FIG. 43.—*Pirates quadrinotatus* (Fabr.) (Piratinae). FIG. 44.—*Lisarda* sp. (Salyavatinae). FIG. 45.—*Sphaeridops amaenus* (Lepeletier and Serville) (Sphaeridopinae). FIG. 46.—*Oncerotrachelus acuminatus* (Say) (Saicinae). FIG. 47.—*Cethera musiva* (Germar) (Cetherinae). FIG. 48.—*Wygodzinskyella travassosi* (Lent and Wygodzinsky) (Chryxinae). FIG. 49.—*Reduvius personatus* (L.) (Reduviinae). FIG. 50.—*Stenopoda cinerea* Laporte (Stenopodinae). FIG. 51.—*Microlestria fuscicollis* Stal (Reduviinae). FIG. 52.—*Durgana rubra* Stal (Reduviinae). FIG. 53.—*Velitra philippina* Stal (Reduviinae). FIG. 54.—*Pessoaia argentina* Wygodzinsky (Vesciinae). FIG. 55.—*Bactrodes femoratus* (Fabr.) (Bactrodinae). FIG. 56.—*Emesaya brevipennis* (Say) (Emesinae).

In the Saicinae the hamus of *Tagalis inornata* Stål is the short type as noted in the Piratinae and R and M appear to be separate distally, while in *Oncerotrachelus acuminatus* (Say) the hamus is long and R and M are fused distally.

Some of the variation which occurs in the Emesinae is probably a consequence of the marked narrowing of the wings and the accompanying elimination of certain veins and regions of the wing. In general, the hind wing is characterized by the great reduction or loss of the secondary veins but the anal lobe is well developed (fig. 56). Usually the cubital furrow is unbranched and the subcosta is greatly reduced and indistinguishable. The form of the hamus varies; in *Emesaya brevipennis* (Say), *Empicoris rubromaculata* Blackburn, and *Emesopsis nubila* Uhler it is short and angles abruptly toward the ScR vein. In others such as *Stenolemoides arizonensis* (Banks) it is long and extends to nearly the base of the wing. In *Emesaya brevipennis* the m-cu cross-vein is absent and the media is fused to the cubitus for a short distance. *Stenolemoides arizonensis* has the unusual feature of a distally forked RM vein and the distal branch of M is joined to Cu by a cross-vein. In *Ploiaria varipennis* McAtee and Malloch Cu extends little or not at all beyond the m-cu cross vein.

The Bactrodinae (*Bactrodes femoratus* (Fabricius)) have a hind wing quite similar to that of the Emesinae in lacking secondary veins and a branched cubital furrow (fig. 55). However, the wing is different from the emesine wing in having a rather distinct marginal Sc. The Bactrodinae do not have a metacoxal comb and therefore are not at present assigned to the Piratine Complex.

The foregoing characterizations of the venation of the Piratine Complex is based on an examination of the following: *Rasahus biguttatus* (Say), *Melanolestes picipes* Herrich-Schaeffer, *Sirthenea flavipes* Stål, *Ectomocoris* sp., and *Pirates quadrinotatus* Fabricius (Piratinae); *Pessoaia argentina* Wygodzinsky (Vesciinae); *Stenopoda cinerea* Laporte, *Narvesus carolinenis* Stål, *Pygolampis* sp., *Thodelmus impicticornis* Stål, *Oncocephalus pictipes* Champion, *Pnirontis* sp., *Gnathobleda fraudulenta* Stål, and *Ctenotrachelus* sp. (Stenopodinae); *Eupheno histrionicus* (Stål), and *Cethera musiva* (Germar) (Cetherinae); *Petalochirus umbrosus* Herrich-Schaeffer, *Lisarda* sp. and *Salyavata variegata* Amyot and Serville (Salyavatinae); *Wygodzinskyella travassosi* (Lent and Wygodzinsky) (Chryxinae); *Sphaeridops amaenus* Lepeletier and Serville (Sphaeridopinae); *Triatoma protracta* (Uhler), *Rhodnius prolixus* Stål, *Panstrongylus megistus* (Burmeister), and *Cavernicola pilosa* Barber (Triatominae); *Reduvius personatus* Linnaeus, *Aradomorpha championi* Lent and Wygodzinsky, *Staliastes rufus* (Laporte), *Inara alboguttata* Stål, *Apechtia* sp., *Durgana rubra* Stål, *Sminthocoris singularis* (Walker), *Microlestria fuscicollis* Stål, *Pantopsilus longipes* Berg, *Croscius melanopterus* Stål, *Acanthapsis* sp., *Leogorrus* sp., *Velitra philippina* Stål, and *Pasira perpusilla* Walker (Reduviinae); *Oncerotrachelus acuminatus* (Say), and *Tagalis inornata* Stål (Saicinae); *Empicoris rubromaculatas* (Blackburn), *Emesopsis nubilus* Uhler, *Emesaya brevipennis* (Say), *Ploiaria varipennis* McAtee and Malloch, and *Stenolemoides arizonensis* (Banks) (Emesniae).

Characters of the phallus and fore-wing venation show the Harpactocorinae, Apiomerinae, Rhaphidosominae, Tegeinae, and Phonolibinae to be closely related subfamilies; and, in fact, giving subfamily status to some of these groups may not be justified. In addition, the Physoderinae and Tribocephalinae are probably related to this group of subfamilies, which will be designated here as the Harpactocorine Complex. The members of this complex lack a metacoxal comb and are, by and large, sedentary diurnal predators like the members of the Phymatine Complex.

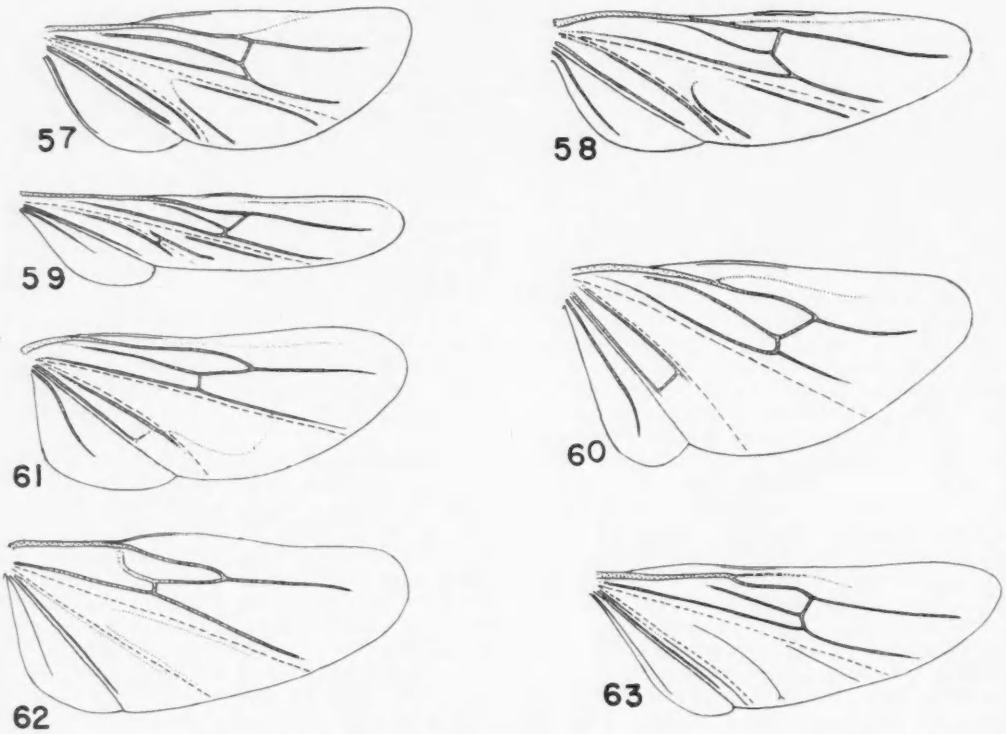
In the hind wing of members of the Harpactocorine Complex (figs. 57-61) the Sc is usually distinct and is submarginal, the hamus is typically rather long and straight and gradually approaches the ScR proximally, the secondary veins vary in development but usually two are present, and the 2d A and anal lobe are usually well developed. The most characteristic feature of the hind wing is the relatively broad postcubital sector and the well separated Pcu and 1st A.

The hind wing of the Physoderinae (fig. 60) and Tribocephalinae (fig. 61) is further characterized by the fact that distally the 1st A curves abruptly forward to meet the Pcu and then appears to cross the posterior cubital furrow where it continues on as a secondary vein extending diagonally across the cubital sector.

Certain features of the abdomen also suggest that the Physoderinae and Tribocephalinae are related to one another and possibly to the Ectrichodinae as well. The Ectrichodinae, however, do not have the characteristic broad postcubital sector of the Harpactorine Complex, but have instead a narrow one (fig. 63) like that of the Piratine Complex.

The foregoing characterizations of the Harpactocorine Complex are based on an examination of the following: *Lopodytes* sp. (Raphidosominae); *Agriocleptes zischkai* Wygodzinsky, *Beharus cylindripes* (Fabricius), *Apiomerus* spp. and *Heniartes erythromerus* Spinola (Apiomerinae); *Acholla multispinosa* (DeGeer), *Arilus cristatus* (Linné), *Pselliopus cinctus* (Fabricius), *Sinea diadema* (Fabricius), *Zelus exsanguis* Stål, *Coranus* sp., *Havinthus rubovarius* Bergroth, *Sphedanolestes* sp., *Bergrothellus rufipes* Miller, *Pristhesancus papuensis* Stål, and *Coranopsis vittata* Horváth (Harpactocorinae); *Physoderes minor* Usinger (Physoderinae); *Opistoplatys australasiae* Westwood and *Tribocephala* sp. (Tribocephalinae); *Pothea haglundii* Stål, *Rhiginia cinctiventris* (Stål), *Ectrychotes* sp. and *Ectrichodia crux* (Thunberg) (Ectrichodiinae).

The Hammacerinae, on the basis of hind wing venation, show no clear affinities to any of the pre-



FIGS. 57 to 63.—Hind wings of Reduviidae of various subfamilies, as follows. FIG. 57.—*Coranus* sp. (Harpactorinae). FIG. 58.—*Heniartes erythromerus* Spinola (Apiomerinae). FIG. 59.—*Lopodytes* sp. (Rhaphidosomatinae). FIG. 60.—*Physoderes minor* Usinger (Physoderinae). FIG. 61.—*Opistoplatys australasiae* Westwood (Tribelocephalinae). FIG. 62.—*Homalocoris varius* Perty (Hammacerinae). FIG. 63.—*Ectrichotes* sp. (Ectrichodiinae).

ceding reduviid subfamilies. Because of the unique features of their genitalia they have, perhaps with some justification, at times been considered to constitute a family unit close to but distinct from the reduviids. The hind wing may be characterized as having an indistinct submarginal Sc, a short hamus which curves toward, and ends abruptly at ScR, two secondary veins, a broad, wedge-shaped, postcubital sector in which the Pcu and 1st A diverge moderately, and a well developed 2d A and anal lobe (fig. 62). In this subfamily the hind-wing venation of *Microtomus cinctipes* (Stål) and *Homalocoris varius* Perty has been studied.

DISCUSSION

It is fully realized that there is grave risk of error and doubtful validity in basing phylogenetic schemes on a single-character complex. It may be useful, however, to indicate certain instances in which the characteristics of the venational pattern of the hind wing appears to ally several of the families of the Cimicomorpha. For the most part the affinities suggested conform with those indicated by other phylogenetic characters (see Drake and Davis 1960).

The hind-wing venation of the Reduviidae is distinctively different from that of other cimicomorphs. This distinctiveness is characterized by the following combination features: The Sc is usually clearly discernible; the cubital sector usually extends nearly to the wing base and contains two secondary veins, and ordinarily the postcubital sector is relatively narrow and in it the Pcu and 1st A are subparallel. The last mentioned feature is the most characteristic of the Reduviidae and, although in several subfamilies the venation of the postcubital sector is highly modified (Holoptilinae and Elasmodeminae) or atypical (Microtominae), it is never similar to that of other cimicomorph families.

The Pachynomidae have characteristics which suggest that they are very closely related to the Reduviidae. However, except for the secondary veins and cubital sector, the hind-wing venation of the species studied (*Punctuis alutaceus*) is not distinctly reduvioid. The postcubital sector is narrow but the pattern of the Pcu and 1st A is more cimicoid than reduvioid.

The Tingidae hind wing resembles that of the reduviids in having a distinct subcosta and two

secondary veins, but in the characteristics of the postcubital sector and its veins, and in the reduction of the anal lobe, tingids resemble the other cimicomorphs.

The remaining families are characterized by a loss of the subcosta, by having only one or no secondary veins, by a cubital sector not extending to the wing base, by having a broad postcubital sector and by the Y- or V-shaped pattern of the Pcu and 1st A.

The hind wings of the Joppeicidae and Thaumastocoridae are remarkably similar and resemble those of the anthocorids and some nabids in the reduction of the 1st A vein.

The apparent distal separation of R and M in some nabids, as well as that described in the microphysids, is contrary to the usual condition of these veins in the Cimicomorpha and is ordinarily a characteristic of the Pentatomomorpha. Since our knowledge of this condition in the microphysids is based entirely on the figure given by McAtee and Malloch (1924), further study of this group is needed. The distal separation of R and M that is found in some of the nabids may constitute a primitive feature since it is quite probable that these veins were separate in the forms ancestoral to the cimicomorphs.

SUMMARY

A reinterpretation of the identity of the veins and regions of the wings of hemiptera has been made based on evidences from tracheation, the relation of veins to axillary sclerites and on a survey of the wing venation of the auchenorrhynchous Homoptera. The principal veins of the fore wing of auchenorrhynchous Homoptera are the C, Sc, R, M, Cu_1, Cu_2, Pcu, 1st A and 2d A. The claval furrow lies in front of or just behind Cu_2. In the heteropterous fore wing, C, Cu_2 and A_2 are absent, and so the principal veins are Sc, R, M, Cu, Pcu, and 1st A. The anal lobe is absent from the fore wing of all Hemiptera, the claval furrow is equivalent to the cubital furrow of the hind wing, and the clavus is equivalent to what is termed the postcubital sector of the hind wing.

The principal veins of the auchenorrhynchous hind wing are the Sc, (which sometimes is accompanied by a reduced C), R, M, Cu_1, Cu_2, Pcu, 1st A, and 2d A. The Cu_2 vein lies just in front of the cubital furrow and the 1st A lies just in front of the anal fold. In the hind wing of the Heteroptera C and Cu_2 are lost and the principal veins are Sc, R, M, Cu, Pcu, 1st A and 2d A. The cubital furrow is often bifid, forming a cubital sector which frequently contains one or two secondary veins. As in the Auchenorrhyncha, the 1st A always lies just in front of the anal fold.

The Hydrocorisae, Amphibicorisae, and Geocorisae each appear to have hind-wing characteristics which serve to distinguish them as groups; the Saldidae, however, are unique, having both an rm and an mcu cross-vein.

A survey of the hind wing venation of the families and subfamilies of the Cimicomorpha indicates the venation in the Miridae, Anthocoridae, Velocipedidae, Thaumastocoridae, and Joppeicidae is of the same basic type. The Nabidae and Microphysidae hind wing resembles that of the above group but, in addition, sometimes has the pentatomomorph characteristic of distally divergent R and V veins. The Tingidae also resemble this group but are different from it in having a distinct Sc and two secondary veins.

A second type of hind-wing venation is found in the Reduviidae and is characterized especially by the narrow postcubital sector containing subparallel Pcu and 1st A veins. The reduvioid family Pachynomidae does not have a distinctly reduvioid hind wing.

Characteristics useful in distinguishing subfamilies of the Cimicomorpha are found in the hind-wing venation of the Nabidae, Anthocoridae and Reduviidae. There appear to be three major groups of reduviid subfamilies, and, in general, characteristics of the hind-wing venation help serve to distinguish each of these groups.

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Biology of the Southwestern Pine Beetle, *Dendroctonus barberi*[1]

CALVIN L. MASSEY[2]

Forest Insect Laboratory, Albuquerque, New Mexico

ABSTRACT

This species is associated with 60% of the insect-caused losses annually in the ponderosa pine type in Arizona and New Mexico. There it has three generations a year. It flies and attacks green trees from early May to October, most intensely in late July and early August; its development from egg through adult requires 50 to 60 days in the summer months. Invariably it attacks the lower parts of the host bole after the tops have been killed by *Ips sp.* The egg galleries are like those of the western pine beetle. In 1957 about 13% of the total emergence was parent adults; the habits of the reemerging adults are not known. Its most important predator is the ostomid beetle *Temnochila virescens;* woodpeckers consume large numbers, but only during the winter months. A 2% emulsion of DDT was found effective in protecting green ponderosa pine against *D. barberi.*

The southwestern pine beetle, *Dendroctonus barberi* Hopk., a native of the Southwest, is one of the most serious pests of ponderosa pine in the region. It is directly associated with approximately 60 percent of the total annual loss caused by insects in the ponderosa pine type. A large portion of the loss occurs in the fringe type of the host species. Losses caused by the insect in association with *Dendroctonus convexifrons* Hopk. and *Ips* spp. increased from 100 million board feet in 1952 to 500 million board feet in 1956. Since that time losses have steadily decreased.

The southwestern pine beetle is native to Arizona, New Mexico and southern parts of California, Nevada, Utah, Colorado, and to northern New Mexico and the Big Bend of Texas.

The primary host is *Pinus ponderosa* Laws. Hopkins (1909) recorded it as rarely occurring in *Pinus edulis* Engelm. and *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco.

Description of Stages.—The life stages of the southwestern pine beetle are shown in figure 1, except for the eggs, which are oblong and pearly white, and similar in shape and color to those of other species of *Dendroctonus.* The southwestern pine beetle is closely related to *Dendroctonus brevicomis* Lec., *D. frontalis* Zimm., *D. arizonicus* Hopk., and *D. mexicanus* Hopk. Studies now in progress may reveal the insect to be synonymous with *D. brevicomis.*

The studies were initiated in 1956 at Bandelier National Monument and continued through 1957. Figure 2 shows ponderosa pine killed by the southwestern pine beetle and associated bark beetles.

[1] Accepted for publication August 25, 1960.

[2] Entomologist, Rocky Mountain Forest & Range Experiment Station, Forest Service, U. S. Department of Agriculture.

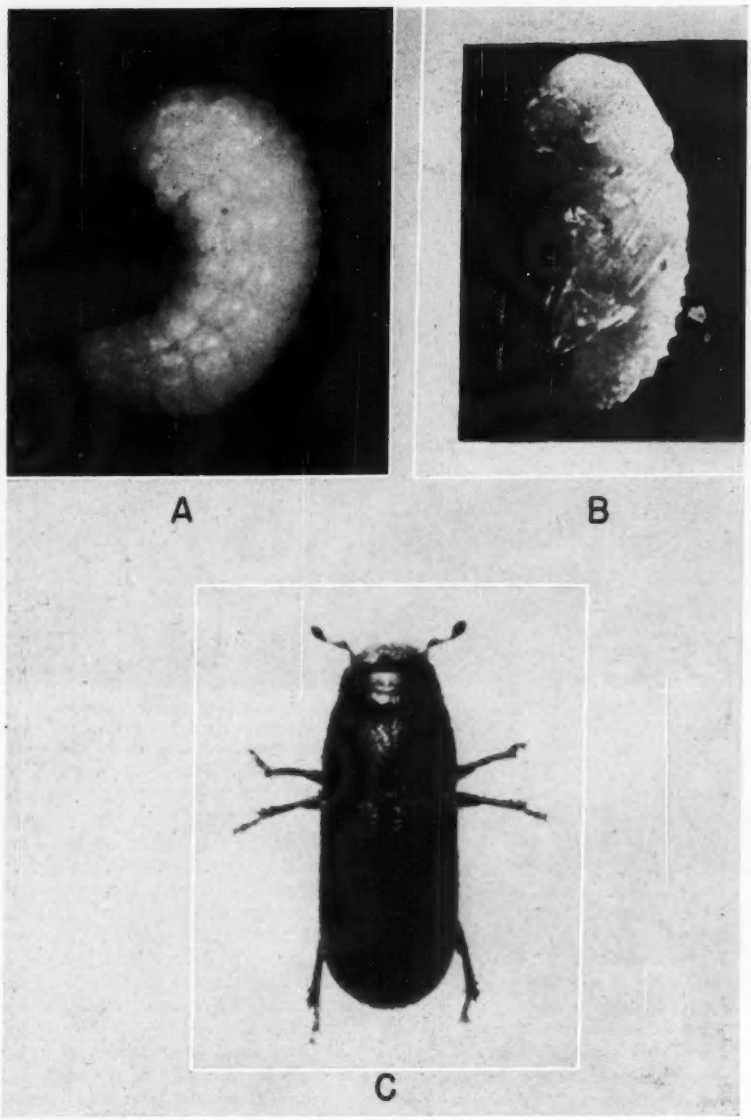

FIG. 1.—Life stages of the southwestern pine beetle. The larva is a compact, cylindrical, legless grub with many transverse folds and wrinkles. The mature larva is approximately ¼ inch long. The pupa is creamy white. The wings, legs, and antennae of the adult are visible through the pupal skin and when nearly mature the light brown of the adult becomes apparent. Callow adults are a light yellowish-brown. Mature adults are deep brown or nearly black.

METHODS OF STUDY

To determine the period of emergence and to obtain information on parasites, predators and associates, trees were caged 1 to 2 weeks after infestation throughout the summer months. Insects were collected weekly from the cages during the field season. Twenty cages were attached to trees in 1956; they covered a bark area of 128.79 sq. ft. In 1957, 21 cages were attached to newly attacked trees. They covered a bark area of 121.69 sq. ft. (figure 3).

To determine the period of attack, three sample plots were established in the study area in early April, 1957. The plots were cruised at weekly inter-

FIG. 2.—Trees killed by the southwestern pine beetle.

vals; each newly infested tree was blazed and numbered.

The rate of brood development was determined by following beetle progress in individual trees from the time of attack to emergence of the adult insects.

Life History.—The studies revealed that the southwestern pine beetle has three generations a year in fringe-type ponderosa pine. During the winter of 1956-57 the insect overwintered as larvae and pupae. These overwintering immature forms completed their development the following spring in the latter part of May and the first part of June. The progeny of these beetles infested trees in late July and early August. Adults resulting from this flight of insects started to emerge during the middle of September; however, emergence was not complete with the onset of cold weather. The spring and summer generations are complete in approximately 2 months. The fall and overwintering generation requires approximately 8 months for completion. A typical chart of the three generations is as follows:

Generation I	*Generation II*	*Generation III*
May. June	July. August	September-March

There is much overlapping of broods. Newly attacked trees occur throughout the spring and summer months. In 1957 they were marked in the study plots from April into September; 5 were marked in April, 7 in May, 43 in June, 64 in July, 48 in August, and 1 in September.

The eggs are laid in the phloem. As the female extends the gallery, small niches are made on either side and one egg deposited in each. The niche is then packed with frass. The average number of eggs per inch in 240 inches of gallery was 5.75; the maximum 8.6. The incubation period is dependent on temperatures. During the summer months the eggs hatch in 7 to 10 days.

On hatching, the larvae feed toward the outer bark. In thin barked trees mature individuals may be found immediately next to the outer bark scales. The larval stage extends over a period of 3 to 4 weeks during the summer months. The larval stage of the overwintering generation may extend over a period of 7 months. Mature larvae form a chamber in the outer bark in which to pupate. The pupal period extends over a period of approximately 1 week in the summer or several months during the winter.

The adult beetles remain in the trees for only a short period after transformation. The beetles make individual emergence holes and fly to susceptible trees immediately after emergence. There are more females than males. Of a total of 4,228 beetles sexed, 2,310 were females, 1,918 were males. Sexual differences in the frons is illustrated in figure 4A,B.

Many adults reemerge shortly after making their egg galleries. In 1957, from a total emergence of approximately 5,100 beetles, 13.7 percent were parent adults. A preponderance of first-emerging parent adults are males. In 1957 infested trees produced

FIG. 3.—Tree cages used in emergence studies of the southwestern pine beetle. The cages were made of No. 16-mesh wire screen and varied in size from 1½ to 2 feet wide to 3½ to 4 feet long. Strips of bark approximately 2 inches wide were peeled from the tree and the edges of the wire were fastened against the wood with roofing nails. The lower part of the screening was funnel-shaped, opening into a pint Mason jar.

an average of 72 beetles per square foot of bark area.

Description of Galleries and Characteristics of Infested Trees.—The egg galleries have a characteristic winding pattern and are nondirectional and netlike in appearance (figure 5), similar to those of the western pine beetle. They are constructed for the most part in the phloem but slightly groove the wood. The larval galleries spread out from the egg gallery into the phloem and outer bark. Larval galleries are usually not visible on the inner surface of the phloem and the outer surface of the wood.

Total lengths of egg gallery were measured within the caged area on 12 trees caged in 1956. The greatest total gallery length was 998 inches in 5.55 square feet of bark. The minimum was 282 inches on 6.08 square feet. The average was 104.45 inches of gallery per square foot.

Infested trees are characteristic in appearance. Upper stems at Bandelier National Monument were initially infested by *Ips oregoni* Eichh., resulting in the fading of the foliage on the upper one-third to two-thirds of the tree. The lower portion of the bole is subsequently attacked by the southwestern pine beetle, with a consequent fading of the lower branches. Infested trees turn a brick-red within 6 weeks to 2 months after the initial ips attack.

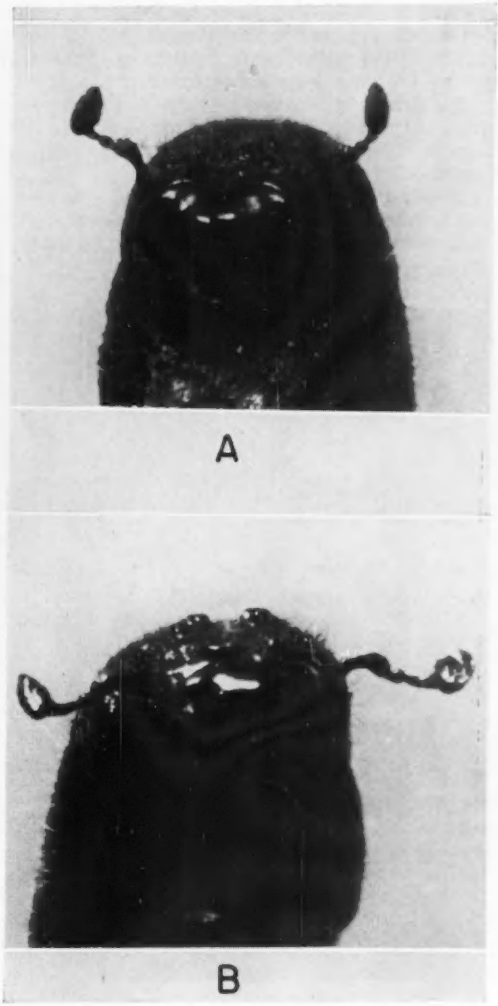

FIG. 4.—*A*, Front female head, southwestern pine beetle. Tubercles faint or lacking.
B, Front male head, southwestern pine beetle. Tubercles prominent.

Ten trees were measured in the study to determine the proportion of stem infested by each beetle. The average length of stem, invariably the upper part, infested with *I. oregoni* was 24.0 feet; the average length infested by the southwestern pine beetle was 22.3 feet. Observations indicate that the southwestern pine beetle prefers trees larger than 12 inches d.b.h. Trees of small diameter were usually infested the full length of the stem with *I. oregoni* and *Ips ponderosae* Sw. or both.

Natural Mortality.—Emergence records from approximately 160 square feet of bark surface indicate that 88 percent of the brood dies before the adults

emerge. This mortality figure was obtained by comparing the average number of eggs laid (590) per square foot of gallery with the average numbers of beetles (72) emerging per square foot.

Parasites and Predators.—Several parasites and predators of the southwestern pine beetle have been identified. Little is known about their effect on beetle populations.

Woodpeckers are important predators. Their feeding is largely confined to the winter months. It is thought that their food during the summer is made up of more easily obtainable insects.

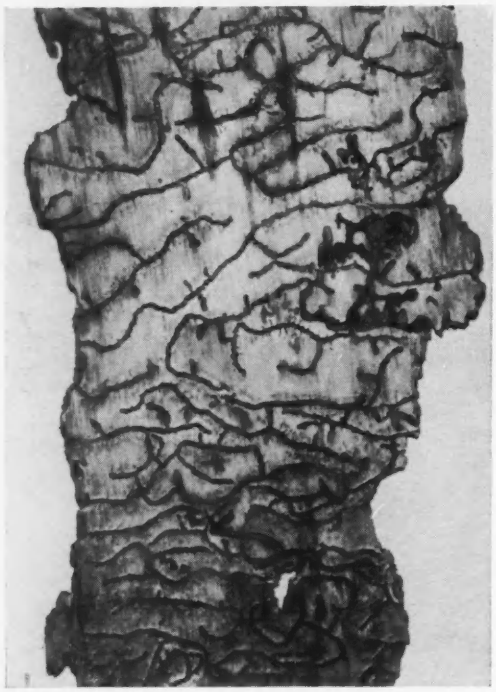

FIG. 5.—Egg galleries of the southwestern pine beetle.

Temnochila virescens Mann. (Ostomidae) is the most important predaceous insect. Larvae of this insect feed upon the immature stages of the southwestern pine beetle throughout the summer months.

The most important hymenopterous parasites collected from caged trees in the study area were *Roptrocerus eccoptogastri* (Ratz.) and *Roptrocerus xylophagorum* (Ratz.).

Aphelenchulus barberus Massey, a nematode parasite of the southwestern pine beetle, infested approximately 3 percent of the population. A total of 346 beetles were examined from 14 trees; only 10 beetles were infested. The effect of the parasite on its host is not known. Other nematodes associated with the insect were *Rhabditis obtusa* Fuchs, *Ektaphelenchus obtusus* Massey, and *Diplogaster pinicola* Thorne.

Associated Insects.—Insects collected from cages were identified by specialists of the Insect Identification Section, Entomology Research Division, ARS.

Scolytid beetles associated with the southwestern pine beetle were *Ips ponderosae* Sw., *Ips oregoni* Eichh., *Dendroctonus valens* Lec., *Dendroctonus convexifrons* Hopk., *Dendroctonus approximatus* Dz., *Orthotomicus ornatus* Sw., *Gnathotrichus denticulatus* Blkm., *Xyleborus scopulorum* Hopk., and *Pityophthorus* spp. *Ips ponderosae* was the most abundant species. In many trees that were initially infested by southwestern pine beetle, subsequent infestations of *I. ponderosae* eliminated the *Dendroctonus barberi* brood.

A complete list of the insects that have been identified as associates of the southwestern pine beetle follows. Many may be predaceous or parasitic; others may be hyperparasites or predators.

HEMIPTERA:

Anthocoridae
Scoloposcelis occidentalis Drake and Harris
Scoloposcelis mississippiensis Drake and Harris
Lygaeidae
Nysius raphanus Howard
Eremocoris setosus Blatchley
Miridae
Rhinacloa forticornis Reuter
Aradidae
Aradus parvicornis Parsh
Aradus sp. near *marginatus* Uhl.

COLEOPTERA:

Staphylinidae (Several species. No specialist available for identification)
Histeridae
Plegaderus sp.
Platysoma sp.
Malachiidae
Attalus sp. prob. *morulus* Lec.
Melyridae
Trichochrous sp.
Cleridae
Cymatodera sp.
Enoclerus nigriventris Lec.
Othniidae
Othnius sp.
Anthicidae
Notoxus sp.
Dermestidae
Anthrenus sp.
Ostomidae
Corticotimus sp.
Temnochila virescens Mann.
Tenebriodes sp.
Airora teres Melsh.
Nitidulidae
Soronia guttulata Lec.
Carpophilus pallipennis Say.
Rhizophagidae
Rhizophagus sp.
Cryptophagidae
Agathengis forticornis Casey
Colydiidae
Aulonium longum Lec.
Lasconotus concavus Casey
Lasconotus sp.
Lathriidae
Enicmus sp.

Tenebrionidae
Tribolium madens Charpentier
Corticeus sp.
Metopolaba sp.
Melandryidae
Rushia sp.
Rushia brevicollis Fall
Anobiidae
Oxoglathus cornutus Lec.
Bostrichidae
Stephanopachys prob. *asperulus* Casey
Cerambycidae
Arhopalus sp. prob. *montanus* Lec.
Acanthocinus obliquus Lec.
Poliaenus sp. prob. *negundo* Schffr.
Curculionidae
Cylindrocopturus sp.
Cossonus sp. prob. *Crenatus* Horn
Cossonus sp.
Cimbocera conspera Fall
Lechriops californicus Lec.
Zascelis inorata Lec.
Rhyncolus nimius Csy.
Tomolips sp.
Orimoderma protracta Horn
Scolytidae
Orthotomicus ornatus Sw.
Ips ponderosae Sw.
Ips oregoni Eichh.
Pityophthorus spp.
Gnathotrichus denticulatus Blkm.
Xyleborus scopulorum Hopk.
Dendroctonus convexifrons Hopk.
Dendroctonus parallelicollis Dz.
Dendroctonus valens Lec.
Hylastes gracilis Lec.

HYMENOPTERA

Formicidae
Campanotus sp.
Campanotus vicinus Mayr.
Liometopum occidentale luctuosum Whlr.
Tapinoma sessile Say.
Monomorium minimum Buckl.
Pteromalidae
Roptrocerus sp.
Roptrocerus eccoptogastri Ratz.
Roptrocerus xylophagorum Ratz.
Chalcidae
Euchalcidia sp.
Hockeria sp.
Braconidae
Chorebus (parasite of Diptera)
Chelonus shoshoneanorum Vier. (parasite of Lepidoptera)
Atanycolus rugosiventris Ashm.
Encyrtidae
Anusiella sp.
Eulophidae
Tetrastichus melanis Burks. (parasite of coccinelids)
Pompilidae
Pompilus parvulus Bks. (parasite of spiders)

DIPTERA:

Omphralidae
Belosta albipilosa Hardy
Belosta sp.
Muscidae
Hylemya sp.
Dolichopodidae
Medeterus spp.
Sarcophagidae
Sarcophaga iherminieri R and D
Stratiomyidae
Zabrachia sp.
Zabrachia polita Coq.
Phoridae
Megaselia sp.
Chloropidae
Hippelates impressus Bene.
Oscinella n. sp.

CONTROL

Research studies on the control of the southwestern pine beetle are centered around sanitation-salvage control methods. At times, however, it may be necessary to protect valuable trees, especially in areas of high recreational use.

To determine if DDT would protect green ponderosa pine from the attacks of this beetle and associate bark beetles, the stems of 475 trees were treated with a 2% emulsion of DDT (Massey 1960). The same trees were treated at the end of May and at the middle of July, and 286 trees were left untreated. An examination of the areas at the end of the season revealed that 103 of the check trees were killed, while only 3 of the treated trees were infested.

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Studies on the Chromosomes of Mosquitoes[1]

OSMOND P. BRELAND[2]

The University of Texas, Austin

ABSTRACT

The prophase and anaphase chromosomes of *Aedes canadensis* Theobald are illustrated, as are the metaphase chromosome complements of 16 other species, as follows: *Culex quinquefasciatus* Say, *C. salinarius* Coquillett, *C. tarsalis* Coquillett, *C. territans* Walker, *Aedes atropalpus* Coquillett, *A. hendersoni* Cockerell, *A. triseriatus* (Say), *A. vexans* (Meigen), *A. zoosophus* Dyar and Knab, *Orthopodomyia alba* Baker, *O. signifera* (Coquillett), *Haemagogus equinus* Theobald, *Anopheles pseudopunctipennis* Theobald, *Culiseta inornata* (Williston), *Psorophora longipalpus* complex, and *Toxorhynchites rutilans septentrionalis* (Dyar and Knab). Additional species examined but not illustrated include *Culex restuans* Theobald, *C. erraticus* Dyar and Knab, *C. coronator* Dyar and Knab, *Aedes sollicitans* (Walker), *Uranotaenia syntheta* Dyar and Shannon, *Psorophora confinnis* (Lynch Arribalzaga), and *P. discolor* (Coquillett). The chromosomes of 16 of these species had not previously been examined. The number $2n = 6$ was found in all species studied. Distinctive chromosome complements were found at prophase in *O. alba*, *O. signifera*, and *T. r. septentrionalis*, and at metaphase for *Anopheles pseudopunctipennis*. Except for this last, the chromosome complements of the species examined at metaphase are quite similar. Mitosis in *Culex salinarius* is illustrated and briefly compared with that previously reported for *C. pipiens*. These studies were made on brain tissue of prepupae, using the squash technique with aceto-orcein as the stain, and these techniques are discussed. Future work suggested includes studies of salivary gland chromosomes and of meiosis, continued search for unique karyotypes, the use of different tissues and techniques, and studies of mitotic stages other than metaphase.

From several standpoints mosquitoes have probably been studied as intensively as any other group of insects. Most of this work, however, has dealt with disease transmission, taxonomy, biology and control; comparatively little is known of the cytology of the group. Stevens (1910, 1911) was one of the first to study mosquitoes cytologically, and since that time, sporadic papers have appeared from time to time. Some of the most important of these articles will be noted later.

Kitzmiller (1953) gave an excellent review of the cytological work that had been done on mosquitoes up to the time his paper was published. When the paper was written chromosome studies had been made of only 12 species of mosquitoes in the United States. Kitzmiller and Frizzi (1954) added one species from this country, and Breland (1959) noted the chromosomal complement of three others, two of which were new. Thus of more than 135 species and subspecies of mosquitoes in the United States, information on the cytology of only 15 has been published at this writing. On a world-wide basis, the percentage of species of which we have cytological knowledge is considerably lower. There are more than 2400 species and subspecies of mosquitoes in the world (Stone et al. 1959) and of this number, the chromosomes of only some 35 to 40 species have been studied at all (Kitzmiller, loc. cit.; Makino 1951).

The numbers of species cited upon which some cytological knowledge is available, even though they are comparatively few, actually appear more imposing than is warranted. The bulk of the work has been done with two species groups, the *Culex pipiens* complex (e.g., Berger 1938; Grell 1946a, 1946b; Kitzmiller 1954; Callan and Montalenti 1947; Whiting 1917) and the *Anopheles maculipennis* complex (e.g., Frizzi 1947a, 1947b, 1947c; Frizzi and Kitzmiller 1959).

At one time the study of chromosomes was relatively difficult and time consuming, but by the use of the so-called squash technique, preliminary results can be obtained rather quickly. In view of this fact, and the current work on mosquito genetics and insecticide resistence being done in several laboratories, it is surprising that so few species of mosquitoes have been investigated cytologically. The squash technique has its limitations, but no other known procedure can compare with it for rapid preliminary investigations. It is hoped that the present paper will help to stimulate interest in the cytology of this very important group of insects.

THE PRESENT STUDY

Kitzmiller (loc. cit.) points out the importance of even such "prosaic" knowledge as the chromosome numbers in many different species of mosquitoes. He also states the need for information relative to chromosome morphology, chromosomal variations and details of mitosis and meiosis. It has seemed logical to us to begin a study of mosquito chromosomes by making a survey of the chromosome complements of all available species before studying details of particular species. This study was begun, and a preliminary article was published describing the techniques and the chromosome numbers of the species *Orthopodomyia alba* Baker, *O. signifera* (Coquillett), and *Culiseta* (= Theobaldia) *inornata* (Williston) (Breland 1959). Since that time more species have been surveyed, and our techniques have been modified and improved. One objective of the present paper is to describe the presently used tech-

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niques which have given us better results than those used in our earlier work.

Another broad objective of this paper is to demonstrate the results that can be obtained within a comparatively short time, using relatively simple procedures. The results are shown in the accompanying photographs. The figures of chromosomes are all reproduced at approximately the same magnification so that more accurate comparisons can be made.

A third objective is to suggest future work in the hope that other investigators will be encouraged to apply these or similar techniques to other species of mosquitoes, other tissues, and other organisms.

In examining the accompanying figures, one should recall that mosquitoes, as well as other Diptera that have been studied cytologically, exhibit somatic pairing. This is a phenomenon in which there is a close association between homologous chromosomes during mitotic divisions in both the soma and germ cells. Somatic pairing has been reported in several groups of plants and animals (e.g., Boss 1955), but so far as animals are concerned, the occurrence of the phenomenon has been questioned in groups other than in the Diptera (White 1954).

In the discussion to follow, no mention is made of the photographic techniques used, since photographic setups differ in different laboratories. We shall be glad, however, to hear from anyone who is interested in the photographic procedures that we use.

TECHNIQUES

The procedures outlined herein are obviously not completely new. They consist for the most part of modifications of standard techniques that have been used in other groups of organisms. We believe, however, that these modifications will give better results with mosquitoes than the techniques used for other organisms. Future workers with mosquitoes or other organisms should experiment with other formulations and techniques. Formulas for materials to be mentioned will be given later.

All species examined, except *Haemagogus equinus* Theobald, were collected in nature at or near Austin, Texas, usually as larvae in various stages of development. The specimens of *H. equinus* were from a laboratory colony and were kindly furnished by Dr. Paul Woke. Collected specimens were brought into the laboratory and allowed to develop to the proper stage in enamel rearing pans. The larvae were reared in pond water, and powdered dog food and brewer's yeast were sprinkled occasionally on the water surface.

Our studies have been in the nature of a survey in which we have examined the chromosome complement of all species of mosquitoes available to us up to the time of this writing. This we have done by the use of the so-called squash technique on the brains of prepupae. The squash technique was first developed by plant cytologists, one of the first publications in this connection being that of Belling (1926). Painter (1934) used this method for a study of *Drosophila* salivary chromosomes, and within recent years, the method has been widely used in the study of many plant and animal tissues.

Brain tissue was selected because the brain is used successfully for routine chromosome surveys in *Drosophila*, and it has been used in various other Diptera (e.g., Boyes and Slatis 1954, and earlier papers by Boyes). Obviously the most successful studies can be made at a time when the brain cells are in active stages of division. In mosquitoes—and perhaps in other insects also—rapid cell divisions occur in the brain cells intermittently. Thus it is important that the stage in the life cycle that is selected for study is one in which the brain cells are undergoing division.

In mosquitoes the prepupal stage is the one in which we have been most successful in finding mitotic figures in the brain. This stage occurs near the end of the last larval stage or instar, just before pupation takes place. The prepupal stage can be easily distinguished because at this time certain developing pupal features can be seen through the larval integument. The pupal trumpets are among the first pupal structures to become visible; they appear in the first thoracic segment of the larva (fig. 1). The

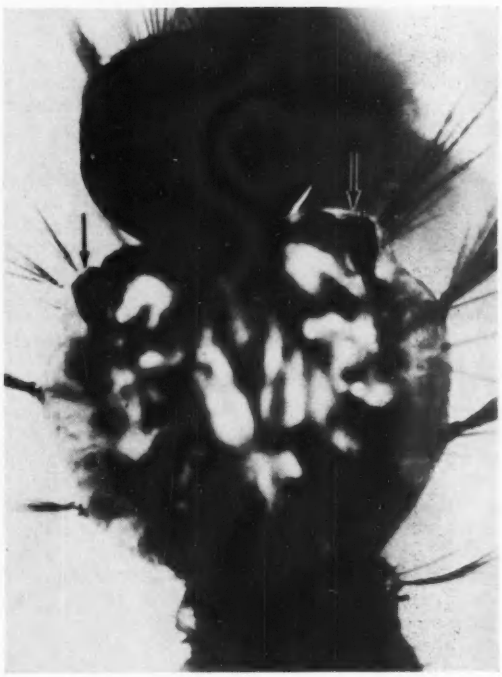

FIG. 1.—Prepupal stage of a mosquito, showing position of pupal trumpets, designated by arrows. This is a late prepupa, as shown by the dark color of the trumpets. In most species more mitotic figures can be found in the brain of an early prepupa, when the trumpets are light in color.

pupal trumpets are at first light in color, but become darker as development proceeds. We routinely dissect at an early prepupal stage. At this time the trumpets appear as light spots, and they are sometimes difficult to distinguish; with experience one has considerable less difficulty.

The larva in fig. 1 shows the position of the pupal trumpets, but this is a late prepupa as can be determined by the dark color of the trumpets. This stage, rather than an early prepupa, is shown because the light-colored trumpets of an early prepupa would not show up well on a photograph.

Usually it is not possible to distinguish a prepupa with the unaided eye, and consequently, a low-power (about 20X to 30X) dissecting microscope is used. A living specimen is placed dorsal side up in a drop of water on a microscope slide and examined. If the specimen is an early prepupa, the head is removed with dissecting needles. This is done by placing one needle on the thorax, another needle between the head and thorax, and pushing the head anteriorly with the second needle. Care is taken not to crush or distort the head capsule. The anterior end of the digestive tract and the salivary glands often are pulled from the thorax as the head is pushed forward. If this occurs, the digestive tract is severed as close to the head as possible and the head transferred to modified Carnoy's fluid. Dissections for salivary glands are often done by slight modifications of this method (Breland 1959).

The head is placed in fixing fluid for two reasons: first, to make the brain opaque so that it can be more easily differentiated from the surrounding tissue, and secondly, to harden the brain so that it is more easily removed. For most species, 45 seconds to 1 minute's exposure to Carnoy's fixative is sufficient to attain these objectives; longer exposure time may cause the brain to become too hard for proper squashing. Certain species, however, such as *Toxorhynchites rutilus septentrionalis* (Dyar and Knab), which have a large amount of muscle tissue in the head, require several minutes. One of the depressions in a bacterial counting plate is used as a container for the fixative.

The head is removed from the fixative with a pipette and placed on a microscope slide; excess fixative is removed with filter paper. A drop of Belar's saline is added, and the brain dissected from the head, using dissecting needles. Relatively low magnification of a dissecting microscope, 20X to 30X is used, occasionally switching to a higher magnification to check results. Some of our technicians prefer small dissecting needles such as sharpened insect pins, but the writer obtains good results with sharpened, standard-size, dissecting needles.

In dissecting, the head is oriented with the anterior part of the head up and the mouth region toward the dissector. One dissecting needle is placed in the mouth and is used to hold the head in place by pressing on the posterior wall of the mouth cavity. The second dissecting needle is then inserted into the mouth above the first needle and pushed anteriorly to cause the head capsule to split laterally. As the head capsule splits, the brain will usually remain in that portion of the head that contains the eyes. An effort is made to cause the splits to occur anterior or posterior to the eyes, since if they pass through the eyes the brain usually is damaged.

The brain lies transversely across the head capsule, between the eyes on the dorsal side, the side opposite the mouth. The size and shape of the brain and the amount of associated tissue vary with the species, and with the stage of development. It usually has two, somewhat spindle-shaped lobes—each of which may be partially divided by a constriction—from which nerves pass to the eyes. Circumenteric commissures pass ventrally around the digestive tract and join a ventral subenteric ganglion (fig. 2). At this stage of dissection, the anterior part of the digestive tract is usually still present and held in place by the circumenteric commissures.

The nerves from the brain that pass to each eye are broken and the remainder of the head capsule and the surrounding tissue, including the anterior part of the digestive tract, is removed. It is sometimes necessary to break the commissures to remove the digestive tract.

The slide used for the dissection is also used for staining, since one is more likely to lose the brain if it is transferred to another slide. All the debris is removed from the slide and the brain oriented near the center of the slide. Excess saline is removed with filter paper. During this process care is taken that the brain is not drawn to the filter paper and lost.

A drop of aceto-orcein is added to the brain and a

FIG. 2.—Posterior view of head of mosquito larva, partially dissected, to show brain.

small metal ring is placed around the drop of stain. A cover slip is placed over the top of the metal ring to prevent the evaporation of the stain.

For most species of *Aedes, Culex, Orthopodomyia* and *Psorophora* we have examined, exposure to aceto-orcein for 20 to 45 minutes will usually give a satisfactory stain. However, certain species, such as the few species of *Anopheles* we have studied and *Toxorhynchites r. septentrionalis,* require a longer time. These species are usually stained for 1 1/2 to 3 hours.

After the brain has been exposed to the stain sufficiently, the excess stain is removed with filter paper. Sometimes the brain cannot be seen in the dark stain, and under these circumstances, the slide is placed under a dissecting microscope and the stain is dispersed with a dissecting needle by spreading from the edges of the stain. The brain will appear as the stain is spread.

A drop of 50 percent acetic acid is added to the brain, excess stain and most of the acetic acid is removed with filter paper, and another drop of acetic acid is added. The brain is then oriented near the center of the slide, and a large square cover slip (18 mm. to 22 mm.) is applied so that the brain is near the center of the cover slip. This can usually be accomplished if one edge of the cover slip is placed on the slide in the proper position, and the free edge gently lowered by the use of a dissecting needle.

The brain is squashed by placing a strip of filter paper over the cover slip and applying pressure to the cover slip with the thumb. Maximum pressure is usually desirable, and this is obtained by placing one thumb over the other and applying pressure with both hands. Care is taken not to move the cover slip, since movement will ruin the preparation. With experience one can often estimate reasonably accurately whether or not a squash is satisfactory by examining the preparation with the unaided eye, although it is sometimes necessary to examine the slide under a compound microscope at this stage. If the squash is not satisfactory, acetic acid is added to the edge of the cover slip and the squashing is repeated. When the preparation is satisfactory, acetic acid is added to the edge of the cover slip and the slide is sealed.

Slides are sealed with a balsam-paraffin mixture, using a 1/2-inch metal spatula with a straight edge on the end. The end of the spatula is heated red-hot, and the balsam-paraffin mixture is stirred and melted. Some of the melted material will adhere to the end of the spatula and sealing is accomplished by drawing the end of the spatula along one edge of the cover slip, and repeating on the other three sides. The cover slip is held with a finger tip at all times to prevent movement.

From the standpoint of time, the principal variable in the whole procedure is the staining time, which varies somewhat among the different species. For those species which require a relatively short staining time, slides can be completed rapidly. When one becomes proficient in dissection it is possible to start with a living prepupa and have a completed slide within 45 minutes to 1 hour. Well-sealed slides are usable for at least 1 month to 6 weeks, and an occasional slide lasts for several months.

Two final points should be made relative to technique. Some investigators prefer to use aceto-carmine for squashes, but aceto-orcein has given us consistently better results. We have also found it necessary to use synthetic orcein. Synthetic orcein is considerably more expensive than natural orcein, but the results we have obtained have been far superior to those when the natural material was used.

FORMULAS FOR MATERIALS

Modified Carnoy's Fixative.—One-third chloroform, one-third glacial acetic acid, one-third absolute alcohol.

Aceto-Orcein Stain.—Mix 33 ml. distilled water, 33 ml. lactic acid, and 33 ml. glacial acetic acid. Stir in 2 gm. synthetic orcein and heat for about 30 minutes. Do not boil. Stir regularly. Filter stain while hot.

Balsam-Paraffin Sealer.—Canada balsam, 60%; paraffin, 40%. Melt paraffin, stir in balsam, and mix well.

Belar's Saline.—Sodium chloride, 6.0 gm.; potassium chloride, 0.2 gm.; calcium chloride, 0.2 gm.; sodium bicarbonate, 0.2 gm. Add distilled water to make 1 liter.

DISCUSSION

One objective of chromosomal studies should be to gain information relative to evolution and relationships, and for this reason a few statements should be made regarding the taxonomic status of the Family Culicidae, the group in which mosquitoes are included. There is still considerable disagreement among current taxonomic workers as to the insects that should be included in this family, and also as to the major taxonomic divisions that should be recognized.

Edwards (1932) recognized three subfamilies, the Culicinae, the Chaoborinae and the Dixinae. He further subdivided the Culicinae, the so-called true mosquitoes, into three tribes, the Anophelini, the Toxorhynchini (= Megarhini) and the Culicini. Carpenter and LaCasse (1955) followed the classification of Edwards, but in their monograph they included only the Culicinae.

Stone (1956) raised the subfamilies Culicinae, Chaoborinae, and Dixinae to family rank, and this modification has been followed by recent workers (Stone et al. 1959; Thurman 1959). The family Culicidae, as now recognized, is divided into three subfamilies. These are the Anophelinae, which includes the genus *Anopheles* and its relatives *Chagasia* and *Bironella* (the latter two do not occur in the United States); the Toxorhynchinae, including the genus *Toxorhynchites* with a single species and two subspecies in the United States; and the Culicinae,

into which are placed all the other genera of mosquitoes.

The subfamily Culicinae is divided into two tribes, the Sabethini and the Culicini, by some investigators (Stone et al. 1959), and into five by some (Stone 1956; Thurman 1959). In the subfamily Culicinae there are at present 27 recognized genera in the world, and in the list that follows they are grouped according to tribes as recognized by Thurman (loc. cit.). The genera having representatives in the United States are listed in bold-face type.

Sabethini: *Trichoprosopon, Tripteroides, Sabethes,* ***Wyeomyia,*** *Phoniomyia, Limatus, Topomyia, Malaya* (=Harpagomyia).
Uranotaeniini: *Zeugnomyia, Hodgesia,* ***Uranotaenia.***
Culisetini: ***Orthopodomyia,*** *Aedomyia, Ficalbia,* ***Mansonia, Culiseta*** *(=Theobaldia).*
Aedini: *Heizmannia,* ***Haemagogus,*** *Eretmapodites, Armigeres, Udaya, Ayurakitia,* ***Psorophora, Aedes,*** *Opifex.*
Culicini: ***Culex, Deinocrites.***

The karyotypes of one or more species in 9 of the 12 genera found in the United States have been examined by other workers or by us. So far as can be determined, no species of *Deinocerites, Mansonia* or *Wyeomyia* has been examined cytologically. The species and genera that have been studied include representatives of all the major taxa listed above with one exception, the tribe Sabethini, in which *Wyeomyia* is included, and so far as known no member of this tribe has been investigated cytologically.

One might expect that several kinds of karyotypes would have been discovered in the Culicidae by even the relatively small amount of cytological work that has been done, since several genera, tribes and subfamilies have been involved. Except for species of *Anopheles,* to be mentioned again later, this possibility has not been realized.

All species of mosquitoes for which the chromosome numbers have been definitely established have the number $2n = 6$. In some of the earlier work both a larger and a smaller number have been reported, but as yet these reports have not been confirmed. For example, Stevens (1911) gave the number $2n = 12$ for a supposed unidentified species of *Anopheles.* Stevens, however, did her work with pupae, and had neither larvae nor adults for positive identification. Taylor (1914) reported the number $2n = 3$ for *Culex pipiens* L., and Carter (1918) gave the number $2n = 4$ for *Aedes aegypti* (L.) (= *Stegomyia fasciata* Fab.). Since these original publications were made, the significance of somatic pairing and polyploid cells in the Culicidae have been more fully recognized; these phenomena may have been responsible for the reports of diploid numbers other than six. The relative sizes of the chromosome pairs in most species are also similar in that there is one small pair and two somewhat larger pair.

Mitosis.—Various aspects of mitosis have been touched upon in several species of mosquitoes, but to date, the most complete studies have been made on the so-called northern house mosquito, *Culex pipiens pipiens* L. (e.g., Grell 1946a, 1946b; Hance 1917; Whiting 1917).

We have so far not attempted a detailed study of mitosis, but we have examined the various stages in many different species. We feel that at this time certain comparisons between our findings and the results obtained by former workers, as well as certain suggestions and speculations, would be of some value to future investigators. Our most complete series of mitotic stages has been obtained from *Culex salinarius* Coquillett (plates 1 and 2). This species is included in the same subgenus (*Culex*) as *C. pipiens,* but the two are often considered to be in different species groups (e.g., Edwards 1932).

Preliminary studies indicate that the mitotic process is quite similar in *C. pipiens* and *C. salinarius,* although they differ in some details. Some of the differences to be mentioned are obviously the result of different techniques, and perhaps different tissues that have been used. Whiting (loc. cit.) used larval gonads for his studies, whereas Hance (loc. cit.) used somatic tissue including "nervous tissue" and larval limb buds. Both these workers made their studies from paraffin sections, using haematoxylin as a stain. Grell (1946a, 1946b) examined a variety of somatic tissues and employed Feulgen- and haematoxylin-stained paraffin sections, as well as aceto-orcein smears. As has been mentioned previously, we have worked primarily with prepupal brains and aceto-orcein squashes.

We have not routinely seen nuclear membranes, spindle fibers, or nucleoli in our preparations as reported by earlier workers. This is not surprising, however, since aceto-orcein, the stain we have been using, has an affinity for chromosomes rather than for other parts of the cell. In *C. pipiens,* chromatids have been seen at late prophase (Grell) and at metaphase (Hance). Chromatids at these stages have not been observed in our preparations of *C. salinarius.* In fact, one of the few species in which chromatids have been distinguishable as early as metaphase is *Haemagogus equinus* Theobald, a species of mosquito that has been reported from the United States at this writing only in the vicinity of Brownsville, Texas (fig. 3).

Grell called attention to the unstained regions near the center of the chromosomes which were apparently most evident during prophase. These regions, which probably represent the regions of the centromeres, were seen in our studies at prophase (plate 1, fig. 9) and occasionally at metaphase (plate 2, figs. 14 and 15). Neither we nor earlier workers have seen evidence of any differentiation in these unstained regions.

One apparent difference in mitosis in the two species is the time at which the somatically paired homologous chromosomes lose contact with each other. Grell and Hance both state that homologous chromosomes in *C. pipiens* separate at late prophase and apparently do not associate intimately again until

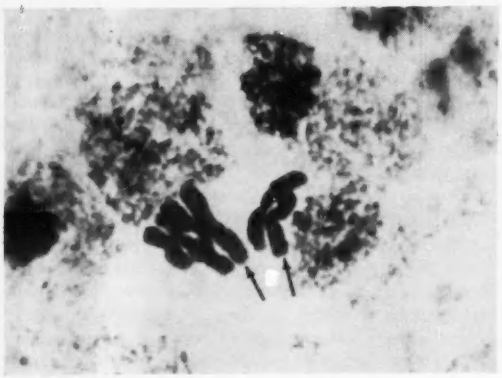

FIG. 3.—Metaphase chromosomes from the brain cells of *Haemagogus equinus* Theobald, showing chromatids. Two obvious chromosomal division regions are designated by arrows. x1,600.

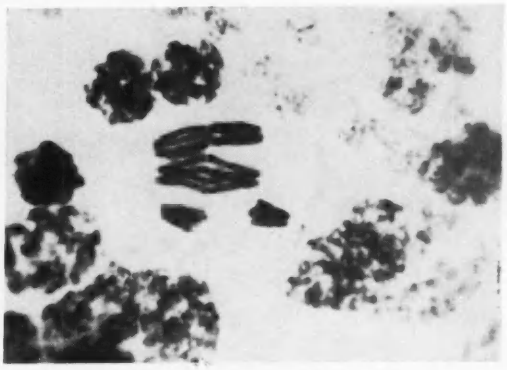

FIG. 4.—Anaphase chromosomes from the brain cells of *Culiseta inornata* (Williston), showing early separation of the smallest pair of chromosomes. x1,600.

anaphase. In our material of *C. salinarius*, however, homologous chromosomes remain in contact until early metaphase (plates 1 and 2). In this connection, the significance of stages such as illustrated in plate 1, fig. 9 is not definitely known at this time; only two of this type have been seen in several slides that have been examined. If these are normal "steps" in the mitotic process, it appears that figures of this type could have one of two explanations: either the time of dissociation of homologous chromosomes varies in different cells (possibly correlated with type of cell), or each group of chromosomes partially disassociates at this stage, then reassociates at a later stage, as in plate 1, figs. 11 and 12. It hardly seems logical that the pressure of the squash could completely account for the disassociation of the chromosomes shown in this figure. The chromosomes shown here are on the same slide and in the same microscopic field at 500X as those shown in plate 1, figs. 11 and 12 and several similar groups, all of which are much more intimately associated.

A few additional points, not previously emphasized by previous workers, should be mentioned at this time. The chromatids of the smallest chromosome pair apparently invariably separate at early anaphase before either of the large pairs. This situation is shown in plate 2, fig. 16. At this stage, the small chromosome pair is sometimes between the two larger pair, and sometimes on one side. This early separation of the smallest chromosome pair has also been noted in several other genera and species, and it may be that this phenomenon occurs in most species (e.g., fig. 4).

There is some evidence that one of the larger pairs of chromosomes separates at anaphase before the other pair (plate 2, figs. 17 and 18). This apparent early separation of one of the larger pairs may be correlated with the fact that at early metaphase homologous chromosome pairs presumably contract and disassociate at different rates (plate 1, fig. 13; plate 2, fig. 14). Probably the smallest pair of chromosomes contracts and dissociates before either of the larger pairs, but in our material we have not seen any figures that fully support this idea. This same situation has been observed in other species (e.g., fig. 5).

FIG. 5.—Anaphase chromosomes from brain cells of *Aedes canadensis* (Theobald), showing late separation of one of the larger pairs of chromosomes. x1,600.

As we have noted in the captions, all of the photographs showing stages in mitosis (plates 1 and 2) were taken from a single slide. This preparation was exposed to aceto-orcein for 45 minutes. However, we have found supporting evidence for most of the suggestions and speculations in several to many other figures and slides. The lone exception is the situation illustrated in plate 1, fig. 9. In this case we have noted only one additional similar figure, and we thus do not know whether or not this stage is a normal part of mitosis in *Culex salinarius*. This almost complete disassociation of homologous chromosomes has also been seen occasionally at prophase in several other species (e.g., *Culiseta inornata*, fig.

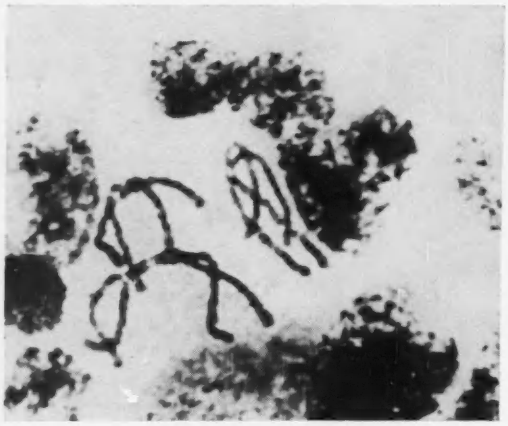

FIG. 6.—Prophase chromosomes from brain cells of *Culiseta inornata* (Williston), showing partial disassociation of homologous chromosomes. x1,600.

6) and it may be that at certain times during prophase the homologous chromosomes do not have as strong an attraction for each other as at other stages.

Metaphase Stages (plates 3-5).—It is well known that metaphase stages are emphasized in making chromosome surveys and in making chromosome counts. We have thus to date accumulated more data and photographs on this stage than on the other mitotic stages.

When this study first began, it was thought possible that the chromosome complements of different species and genera might be sufficiently characteristic at metaphase to give supplementary evidence relative to the relationships and evolution of the various groups. With one exception, distinctive chromosome complements at metaphase have not been seen. This one exception is *Anopheles pseudopunctipennis* Theobald, the only species of *Anopheles* of which we have obtained a reasonably good photograph (plate 5, fig. 33). It can be noted that the chromosomes of this species are considerably smaller and of a somewhat different shape than the chromosomes of the other species that are figured. It can easily be seen from the photograph that three pairs of chromosomes occur, each of which has a distinctive size and shape.

The distinctiveness of the *Anopheles* chromosomes shown here is consistent with the findings of other workers, in that the metaphase chromosomes of the species of *Anopheles* that have been studied have been different than those of other groups of mosquitoes (e.g., Frizzi and Kitzmiller 1959; Kitzmiller 1953). These workers have also reported two types of chromosome complements among the various species of *Anopheles* they have examined. Some photographs have been published of the chromosome complements of *Anopheles* (e.g., Frizzi 1947c) and others have been drawn and/or described (e.g., Kitzmiller 1953; Kitzmiller and Frizzi 1954). The two types of metaphase chromosome complements described by Frizzi and Kitzmiller are as follows: The one characteristic of most species of the so-called *maculipennis* complex consists of two large pairs of v-shaped chromosomes, with equal arms and about the same size, and one pair of smaller rods. Each of the rods has a slight enlargement at the end which has been interpreted by some (see below) as heterochromosomes or sex chromosomes. The other type of chromosome complement is characteristic of *Anopheles claviger* (Meigen) (a species that occurs in Europe) and *Anopheles quadrimaculatus* Say, an American species. Two large v-shaped pairs, similar to those of the *maculipennis* complex, occur, and two much smaller dot-like chromosomes.

The *Anopheles pseudopunctipennis* chromosomes shown here (plate 5, fig. 33) represent a third type of chromosome complement among the *Anopheles*. Three sizes of chromosomes occur, the largest pair of which has definitely unequal arms. The arms of the smaller pair are also unequal. It is believed, therefore, that among the species of *Anopheles* a study of metaphase chromosomes is likely to supply evidences of relationships of the various groups of species.

We are not nearly as optimistic as to the possible value of a study of the metaphase chromosomes of species other than the Anopheles. An examination of the metaphase chromosomes of the various groups figured here will reveal slight size and shape differences. We do not feel, however, that these slight differences are of much significance. The reasons for this are that there are size differences in the chromosomes of the same individual, and the shapes will vary depending upon the stage of mitosis that is being studied, and upon the relative degree of contraction of the chromosomes.

A major problem in comparing the metaphase chromosomes of two species is in determining that the chromosomes of the two groups are at the same relative stage of contraction. We have noted previously that complete disassociation of homologous chromosomes during mitosis occurs later in the process in *Culex salinarius* than in *C. pipiens*. According to Grell's interpretation of her figures (1946b), homologous chromosomes lose contact with each other considerably before maximum contraction has been attained. Thus, in *C. pipiens* complete separation of homologous chromosomes is no indication that the chromosomes have attained their maximum contraction. In *Culex salinarius*, however, in which homologous chromosomes remain in contact for a longer period, we believe that the chromosomes are at or very near their maximum contraction when each of them becomes distinct from its homologue (plate 2, fig. 15).

A late disassociation of homologues also occurs in certain species of *Aedes*, and it is thought that in these species also, complete separation is an indication that the chromosomes are at or near maximum contraction (e.g., plate 4, fig. 29). Probably, therefore, the time of maximum contraction of the

chromosomes varies among the different species, and each species must be studied with this point in mind before the time of maximum contraction can be determined.

In view of the fact that *Toxorhynchites r. septentrionalis* is placed in a distinct subfamily, this is one species that might be expected to have a distinctive chromosome complement as compared with other groups. An examination of plate 5, fig. 36 does reveal slight differences, the most obvious of which is that each of the pair of chromosomes in the middle of the figure has one arm that is somewhat larger and longer than its mate. This difference in arm size is perhaps somewhat more obvious than in certain other species that are figured, although the same situation also occurs in some of the other species (e.g., plate 5, fig. 34). It is not known at present just what the significance of this situation might be, but since it is a comparative feature, its value in identification and in determining relationships is certainly debatable.

Other species, the karyotypes of which have been examined, but for which no acceptable photographs of metaphase have been obtained, include the following: *Culex restuans* Theobald, *Culex erraticus* D. and K., *C. coronator* D. and K., *Aedes canadensis* Theobald, *A. sollicitans* (Walker), *Uranotaenia syntheta* Dyar and Shannon, *Psorophora confinnis* (Lynch Arribalzaga), and *P. discolor* (Coq.). No outstanding features of the chromosomes of these species were noted, but some of these studies were made at the beginning of our work on chromosomes. Future studies may reveal characteristics that were previously overlooked. All of the species listed have the diploid chromosome complement of six.

Our present opinion is that studies of metaphase chromosomes of mosquitoes, other than *Anopheles*, are not as likely to be of as much significance as the examination of other mitotic stages. Many more species of mosquitoes must, of course, be examined before it can be established whether or not this conclusion is valid for all groups of mosquitoes.

Sex Chromosomes.—It is generally agreed that among mosquitoes morphologically distinct heterochromosomes correlated with sex have been demonstrated only in a few species of *Anopheles* (Kitzmiller 1953). However, in view of the results with *Anopheles* and certain relatives of mosquitoes, with the attendant speculation, some of the earlier work with *Culex pipiens* L. suggests the presence of sex chromosomes. Some of this work is of sufficient importance to be mentioned briefly.

White (1949) regarded the Tipulidae (crane flies and relatives) as being cytologically the most primitive of the Diptera. The diploid chromosome complement of some species of this group consists of four pairs of chromosomes, three large pairs of autosomes and a smaller pair that is regarded as sex chromosomes. White suggested that the chromosome complement of mosquitoes could have been derived from the tipuloid type by the incorporation of the smaller sex chromosomes into one of the pairs of autosomes.

White's suggestion is supported by the work of several investigators, including that of Frizzi (1947c), Frolowa (1929), and Stevens (1911). Frolowa did her work with *Chaoborus* (= *Corethra*), family Chaoboridae, a group closely related to mosquitoes and recently classified into a distinct family. She found a pair of heterochromosomes which were sometimes free and sometimes attached to the smallest pair of autosomes. These were visible mostly at prophase stages, and were seldom seen at metaphase. In the *Anopheles* studied by Frizzi and Stevens, the elements interpreted as being sex chromosomes are also attached to the smallest pair of autosomes. These elements are visible at metaphase. In both *Anopheles* and *Chaoborus* the supposed sex chromosomes are equal in size in females, unequal in males.

Stevens (1910) originally reported the presence of heterochromosomes in an unidentified species of *Culex*, but later (1911) stated that further study failed to show these elements in *Culex*. She speculated that the heterochromosomes originally reported had been seen in an *Anopheles*. Whiting (1917) stated that his findings with respect to heterochromosomes in *Culex pipiens* were inconclusive. However, the figures of his so-called "terminal granules" that occur in prophase of both spermatogonia and oogonia appear strikingly similar to the situation seen by Frolowa in *Chaoborus*. Whiting stated in passing that the granules in the oogonia could be sexual elements, but he disregarded this possibility in his discussion of the situation.

We have recently found a situation similar to those in *Chaoborus*, and in Whiting's "terminal granules," in two species of *Orthopodomyia*, mosquitoes that breed primarily in tree holes (plate 6, fig. 37, 38). The elements that may represent sex chromosomes have been found primarily in prophase stages of the prepupal brain. An argument against these objects being comparable to the so-called sex elements as found in *Anopheles* and *Chaoborus* can be made, since in *Orthopodomyia* they are associated with a pair of the larger, rather than the smaller, chromosomes. We do not believe, however, that this argument in itself should exclude our "granules" from consideration as possible sex elements. On morphological grounds, the genera *Anopheles* and *Orthopodomyia* are included in distinct subfamilies, and *Chaoborus* is now considered to belong to a family distinct from the Culicidae. The possible incorporation of sex chromosomes into a pair of autosomes is a rather unusual phenomenon, and it seems possible that in relatively unrelated groups the situation could have been accomplished in different ways. Indeed, such differences in chromosome complements could partially account for different morphological features of the groups involved.

Whatever may be the true connection between these objects and sex, we believe that the elements may be regarded as satellites, which in most in-

stances at least are attached to a pair of the larger chromosomes. A faint indication of such an attachment can be seen in plate 6, fig. 37. We also believe that as the chromosomes condense the satellites become incorporated into the chromosomes to which they are attached—hence the satellites are not routinely visible at metaphase.

The two elements or satellites in our preparations are sometimes similar in size, and sometimes of unequal size, but so far we have had difficulties in correlating these size differences with sex. The gonads of the prepupae of these species of *Orthopodomyia* are so undeveloped at this stage that they are sometimes difficult to find, and if found, are often difficult to differentiate. Perhaps with experience this problem will be solved.

SUGGESTIONS FOR FUTURE WORK

It should be obvious from the preceding discussion that any observation relative to the chromosome complement of species of mosquitoes not previously examined would be worthwhile. Also, that the surface has barely been scratched even in most species that have been examined. Chromosome counts should certainly be made on all possible species, and the numbers reported.

Future studies may reveal species of mosquitoes with radically different metaphase chromosomes, but except for some species of *Anopheles*, this has not occurred up to the present time. Present indications are that more chromosomal features characteristic of species, and perhaps of genera, will be found in mitotic stages other than metaphase. Well-spread anaphase stages, such as fig. 7, should receive close attention. In fact we have recently suggested that differences in the anaphase stages of two very similar species of mosquitoes are significant (Breland 1960). Unfortunately, such figures are rare in most preparations, but when they do occur, full advantage should be taken of the situation.

Distinctive prophase stages have been found in some groups as illustrated by plate 6, figs. 37, 38, 39. It will be noted that small satellites occur in both species of *Orthopodomyia*, and that in *Toxorhynchites rutilus septentrionalis*, larger objects, apparently comparable to satellites, occur that are independent of the larger chromosomes at this stage. The two species of *Orthopodomyia* cannot be distinguished from each other on the basis of the prophase chromosomes, but the two can obviously be distinguished from *T. septentrionalis*. We have no indication whether or not the extra elements in *T. septentrionalis* may be sex chromosomes. They are apparently incorporated within one of the larger pairs of chromosomes as the chromosomes condense, since these elements have not been seen at metaphase.

The possibility has been considered that the so-called satellites and extra elements seen in certain species might be the result of chromosome breaks that are caused by pressure when the squash preparation is made. Possibly the pressure contributes something to the final prophase configuration in these species, but if pressure were the complete answer, many kinds and sizes of breaks should occur, and similar elements should be present in other species. These situations do not routinely occur. The extra elements occur in a high percentage of prophase stages in *Orthopodomyia* and *Toxorhynchites*, often when there are no breaks in the other chromosome elements. Conversely, similar elements have not been seen in other species (plate 6, figs. 40, 41, 42). It is believed, therefore, that the satellites and extra elements are highly significant features of the prophase chromosome complements of the species in which they occur.

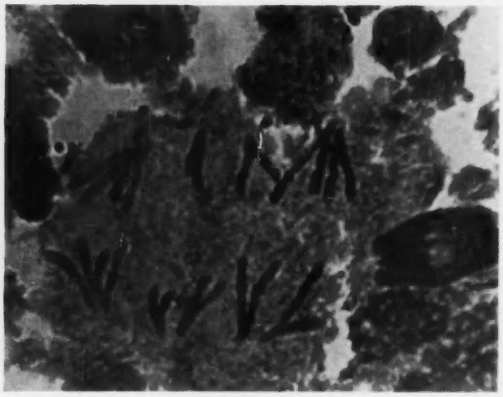

FIG. 7.—Well-spread anaphase chromosomes from brain cells of *Aedes triseriatus* (Say). In preparations of this type, the relative arm lengths of the chromosomes can be seen. Note the earlier anaphase figure to the right. x1,600.

Details of meiosis in mosquitoes should be studied carefully, since many features of evolutionary significance have been found in many groups of organisms by such investigations. (See Smith 1960, White 1957, for concise reviews of findings in insects.) An investigation of meiosis might also help to solve the problem of sex chromosomes in mosquitoes. Our preliminary studies have shown that there is considerable variation in gonad development in different species at a given stage, and indications are that the stage when meiosis occurs also varies among the different groups.

In some respects, studies of salivary and salivary type chromosomes seem to offer the most attractive field for future investigators. The possible results of such work are well illustrated by several papers of Frizzi (1947a, 1947b) and Frizzi and Kitzmiller (1959). Some preliminary observations in our laboratory show that several species have definitely banded, and perhaps usuable, chromosomes in their salivary glands and/or malpighian tubles. Frizzi (loc. cit.) pointed out that so far as laboratory-reared specimens are concerned it is necessary to feed the larvae a special diet in order for them to have well-banded salivary chromosomes. It appears

probable that fourth-instar larvae collected in nature would have well-banded chromosomes, although it is believed that a primary problem in this connection is in selecting the right developmental stage for study. The best stages for best results probably vary in different species, and intensive study will probably be necessary in order to determine what these stages might be.

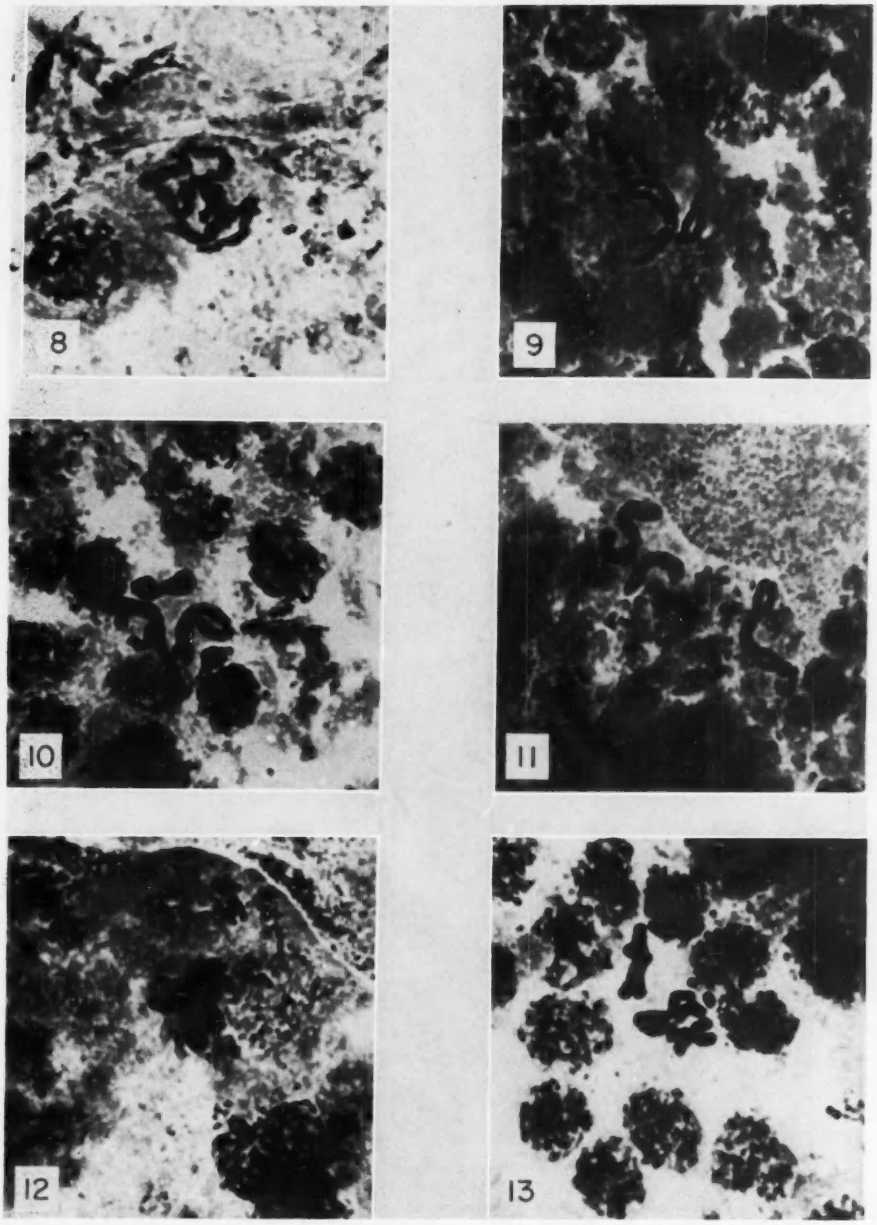

PLATE 1.—Stages in mitosis in the brain cells of *Culex salinarius* Coquillett. x1,600. All the photographs on Plates 1 and 2 were taken from one slide. FIGS. 8-11.—Prophase. FIGS. 12-13.—Metaphase. In fig. 9 the photograph does not show the third pair of chromosomes, which was at the same stage of dissociation as the other two pairs. In fig. 13 one pair of chromosomes is more intimately associated than the other two pairs.

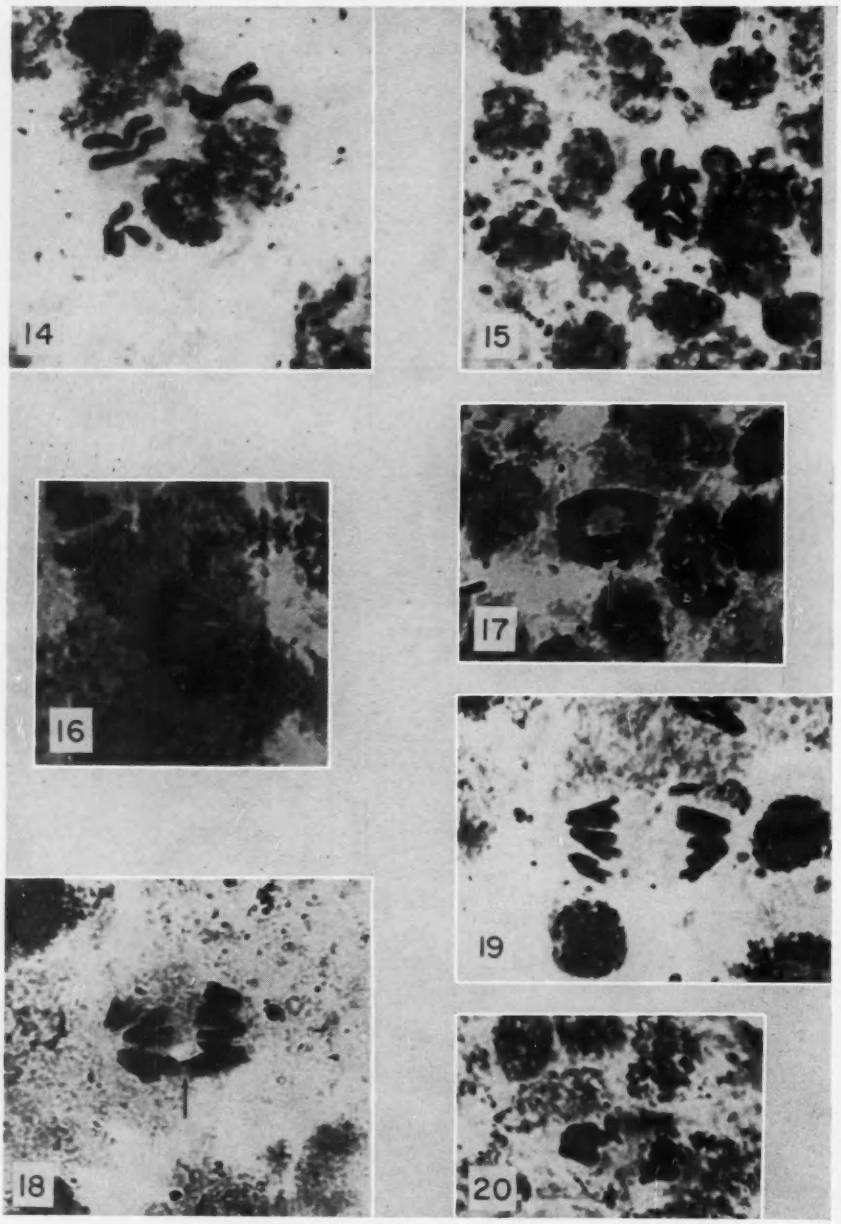

PLATE 2.—Stages in mitosis in the brain cells of *Culex salinarius* Coquillett, x1,600. All the photographs on Plates 1 and 2 were taken from one slide. FIGS. 14-15.—Metaphase. FIGS. 16-19.—Anaphase. FIG. 20.—Telophase. In fig. 16 the smallest pair of chromosomes has separated first; in fig. 17 one pair of large chromosomes has started separating before the other; and in fig. 18 one pair of large chromosomes has completely separated, the other pair still partially attached.

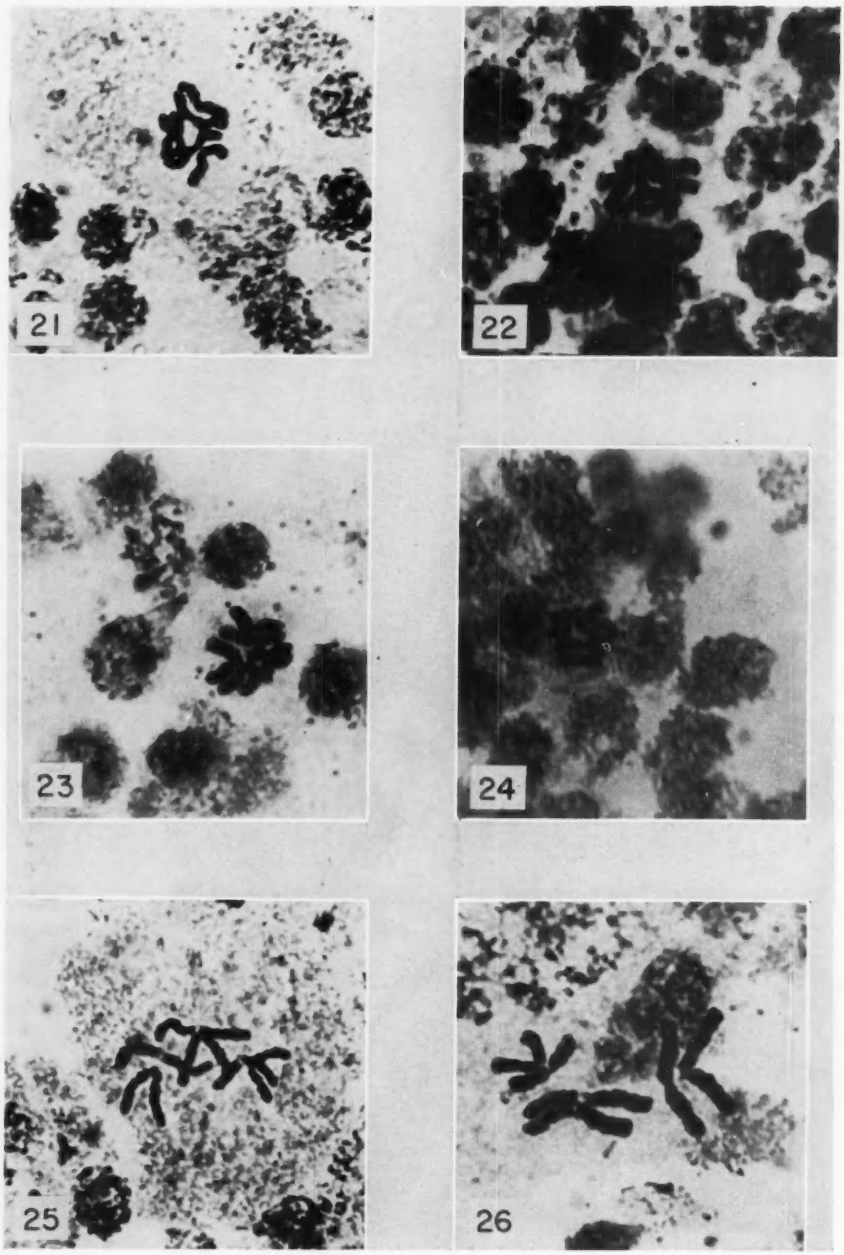

PLATE 3.—Metaphase chromosomes of mosquitoes from brain cells. x1,600. Some of the chromosomes, including those in figures 25 and 26, are probably not at their maximum contraction. FIG. 21.—*Culex quinquefasciatus* Say. FIG. 22.—*Culex salinarius* Coquillett. FIG. 23.—*Culex tarsalis* Coquillett. FIG. 24.—*Culex territans* Walker. FIG. 25.—*Aedes atropalpus* Coquillett. FIG. 26.—*Aedes triseriatus* (Say).

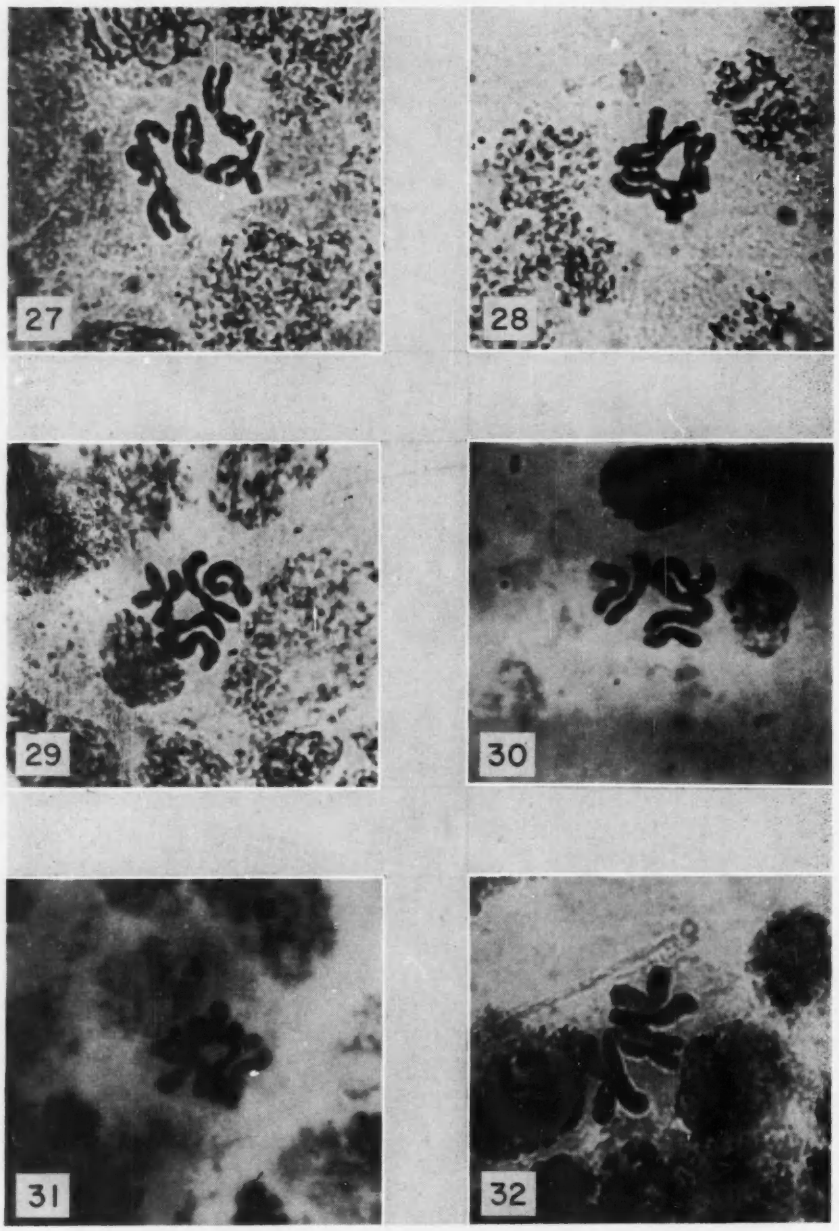

PLATE 4.—Metaphase chromosomes of mosquitoes from brain cells. x1,600. Some of the chromosomes, including those in figures 27 and 28, are probably not at their maximum contraction. FIG. 27.—*Aedes hendersoni* Cockerell. FIG. 28.—*Aedes vexans* (Meigen). FIG. 29.—*Aedes zoosophus* Dyar and Knab. FIG. 30.—*Orthopodomyia alba* Baker. FIG. 31.—*Orthopodomyia signifera* (Coquillett). FIG. 32.—*Haemagogus equinus* Theobald.

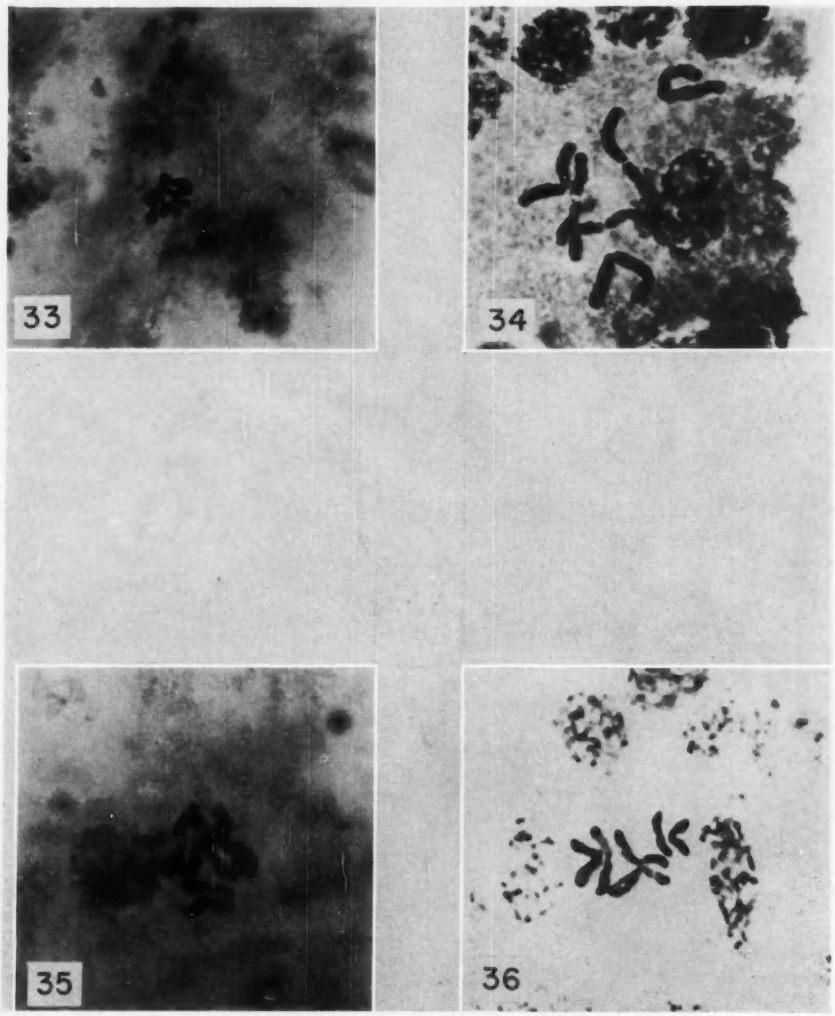

PLATE 5.—Metaphase chromosomes of mosquitoes from brain cells. x1,600. The chromosomes in figure 34 are probably not at their maximum contraction. FIG. 33.—*Anopheles pseudopunctipennis* Theobald. FIG. 34.—*Culiseta inornata* (Williston). FIG. 35.—*Psorophora longipalpus* complex. FIG. 36.—*Toxorhynchites rutilans septentrionalis* (Dyar and Knab).

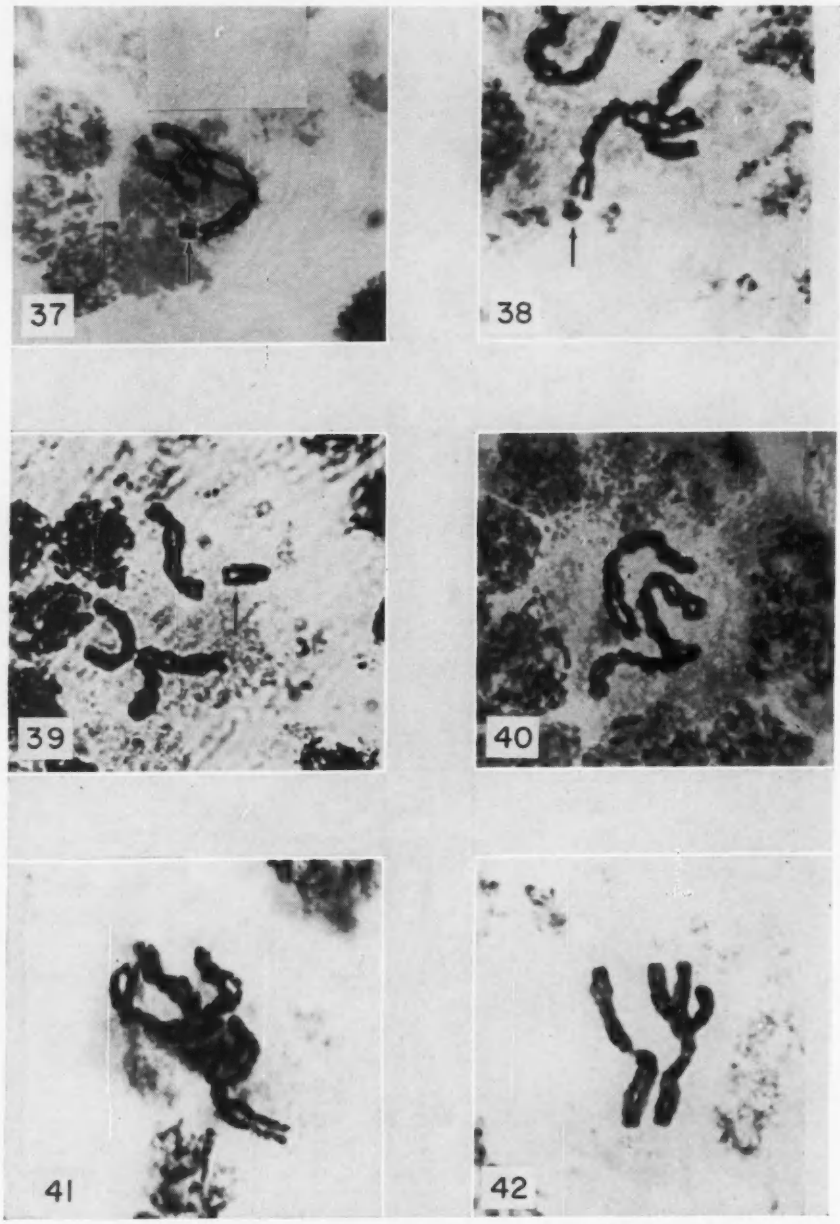

PLATE 6.—Chromosomes from the brain cells of mosquitoes, x1,600. FIGS. 37-39 are prophase stages showing satellites, designated by arrows; figs. 40-42 are comparable prophase stages showing absence of satellites. FIG. 37.—*Orthopodomyia alba* Baker. FIG. 38.—*Orthopodomyia signifera* (Coquillett). FIG. 39.—*Toxorhynchies rutilans septentrionalis* (Dyar and Knab). FIG. 40—*Aedes triseriatus* (Say). FIG. 41.—*Culiseta inornata* (Williston). FIG. 42.—*Aedes canadensis* (Theobald).

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MOSQUITO CATALOG SUPPLEMENT

A Synoptic Catalog of the Mosquitoes of the World, Supplement I (Diptera: Culicidae) by Alan Stone brings the Catalog up to date with corrections and additions. This Supplement appeared in the *Proceedings of the Entomological Society of Washington* 63(1):29-52, March 1961. Price of the Catalog is $7.25, of the Supplement with covers $1.00. When the two are ordered together the price is $8.00. Prices to members when personally purchased are $6.50, 75 cents, and $7.00, respectively. Order from:

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Observations on Egg Production by Aphid Pests of Potato in Maine[1]

W. A. SHANDS,[2] H. E. WAVE,[2,3] AND G. W. SIMPSON[4]

ABSTRACT

Studies in northeastern Maine in 1956 and 1957 showed that egg deposition by *Myzus persicae* (Sulz.) and *Macrosiphum euphorbiae* (Thos.) started soon after the first eggs matured, whereas *Myzus solani* (Kltb.) retained matured eggs until the abdomen was packed and distended. The number of eggs deposited by a healthy ovipara depends upon the duration of favorable weather conditions. Indications are that parasitized aphids lay no eggs.

One objective of the potato-insect investigations in northeastern Maine is to assess the value of aphid egg surveys in making advance estimates of early-season abundance of the four species of aphids commonly infesting potatoes. These are the buckthorn aphid, *Aphis nasturtii* Kltb.; the green peach aphid, *Myzus persicae* (Sulz.); the potato aphid, *Macrosiphum euphorbiae* (Thos.); and the foxglove aphid, *Myzus solani* (Kltb.). The results thus far indicate that such data on the most important primary hosts of the potato and green peach aphids, swamp rose (*Rosa palustris* Marsh.) and Canada plum (*Prunus nigra* Ait.), respectively, have limited value when considered alone. One reason is that other aphids may also deposit eggs on them. Further, our studies for 16 years have revealed an important need for data on the egg-production capacity of these aphids and on the proportion deposited before the onset of winter. This paper is a report of observations on egg production in the foxglove, green peach, and potato aphids in northeastern Maine.

In the fall of 1956 several collections were made of oviparous adults of the foxglove aphid that developed in the greenhouse on artificially infested, caged plants of hemp nettle (*Galeopsis tetrahit* L.), chickweed (*Stellaria media* (L.) Cyrill.), and potato (*Solanum tuberosum* L.). In the fall of 1957 similar adults were taken at random from caged potato plants growing in a field that had been artificially colonized during August. Collections were also made of oviparae of the potato-infesting species observed during field counts on swamp rose, multiflora rose (*Rosa multiflora* Thunb.), Canada plum, and hawkweed (*Hieracium* spp.) at several stations in the central and southern parts of Aroostook County. These aphids were dissected and the eggs counted. The results are summarized in table 1.

The number of eggs per ovipara of the potato aphid rose sharply from September 30, reached a peak about October 10, and then gradually decreased. Less obvious patterns found for the green peach and foxglove aphids may not differ materially.

An outstanding disclosure from the dissections was the difference in egg production and egg retention. Nearly all the eggs found in the foxglove aphid were half grown or larger, whereas most of those in the potato and green peach aphids were less than half grown. Seldom did individual specimens of the last two species hold more than one or two that were half grown or larger. The dissected specimens of the foxglove aphid contained so few eggs less than half grown that those under that size were not counted or included in the data in table 1. Apparently the foxglove aphid retains its eggs longer after reaching full size than do the other species.

Other factors such as sampling procedure could have influenced the observed difference in egg-retention habits. The specimens of the foxglove aphid that were dissected came from whole-plant samples, whereas the others came from leaf samples. Because the green peach and potato aphids leave the foliage to deposit in sites such as bud axils, branch crotches, and bark crevices, the dissected specimens could have consisted predominantly of young adults that had not yet left the leaves to oviposit.

There appear to be several differences among the three species in egg-production and deposition. In the potato and green peach aphids oviposition probably starts soon after the first eggs attain full size, which is soon after the females mature, and it occurs over a rather extended period. Eggs three-fourths grown were found in some maturing oviparae of both species. Apparently these eggs attain their full size soon after the ovipara matures. Nearly full-grown eggs were found in green peach aphids collected on September 18, the date that mature oviparous adults of both species were first observed in 1957. Seldom was more than one full size egg found in either species; in fact relatively few of the females contained even one such egg. This indicates that the eggs are deposited soon after maturing. Oviposition usually occurs well into November, as the aphids continue to mature on the primary hosts throughout the fall.

The duration of the oviposition period of the foxglove aphid cannot be compared with that of the other two species because of its egg-retention habits and the more protected and warmer environments afforded by the low-growing hawkweed. In the field cages maturation on hawkweed began about October 1 in both 1956 and 1957, and oviposition started about October 18 in 1956 and October 11 in 1957. Living oviparous adults have been observed on naturally occurring hawkweed as late as November 22. Oviposition probably continues later in the fall than does that of either the potato aphid or the green peach aphid, which oviposit on taller, more exposed host plants.

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[2] Entomology Research Division, Agricultural Research Service, U.S.D.A.
[3] Resigned August 1958.
[4] Maine Agricultural Experiment Station.

Table 1.—Eggs in oviparous adults of three species of potato-infesting aphids collected in northeastern Maine.

Host plant	Collection date	Number of stations	Number of specimens	Average number of eggs[a] per adult
		Foxglove aphid		
	1956			
Hawkweed[b]	Oct. 19	1	8	4.8
	24	1	7	2.1
	Nov. 7	1	1	4.0
Potato[c]	Oct. 24	1	16	5.9
	Nov. 7	1	94	8.0
Chickweed[c]	Oct. 24	1	28	6.8
	Nov. 7	1	26	7.7
	28	1	17	5.0
Hemp nettle[c]	Oct. 22-24	1	17	13.1
	Nov. 7	1	9	14.8
	1957			
Potato[b]	Oct. 7	1	23	3.2
	11	1	30	3.6
		Potato aphid		
Swamp rose	Sept. 30	4	8	1.8
	Oct. 9-11	7	10	4.2
	21-22	8	51	3.1
Multiflora rose	Oct. 9-11	1	1	8.0
Canada plum	Oct. 9-11	3	3	8.7
	21-22	2	4	4.5
Average, all hosts	Sept. 30	—	—	1.8
	Oct. 9-11	—	—	5.1
	21-22	—	—	3.2
		Green peach aphid		
Canada plum	Sept. 18	1	1	7.0
	30	4	20	3.0
	Oct. 9-11	3	10	3.1

[a] Half grown or larger for foxglove aphid, all sizes for other species.
[b] Caged plants in field.
[c] Caged plants in greenhouse.

The data in table 1 do not permit an estimate of the total number of eggs per female that may be deposited, because the dissected specimens were of unknown age, having been taken at random over a considerable period. They do indicate, however, that each ovipara, regardless of species, may deposit several eggs. According to Horsfall (1924), one adult green peach aphid deposited five eggs. European workers variously report that this aphid deposits from 4 to 10 eggs (Quanjer 1939, Heinze and Profft 1940, Fenjves 1945, Heinze 1951, Müller 1955), and the foxglove aphid as many as 15 (Heinze and Profft 1940). D. Hille Ris Lambers found four to eight eggs in cleared oviparae of the potato aphid in The Netherlands.[5]

The number of eggs deposited per female probably depends largely upon the time of the fall migration and the length of the effective oviposition period—i.e., the total duration of the intermittent periods when the temperature is high enough to promote the development of eggs and permit deposition. This period is governed by the time of the fall migration, the rate of development and the time of maturation, the temperature during the oviposition period, and the start of cold weather. When above-normal temperatures prevail oviposition continues into late fall. On the other hand, a sudden onset of winter may cause an abrupt cessation. At such a time the primary hosts have been infested not only by oviparous adults of differing ages, which may have been ovipositing for various periods, but also by immature and recently matured individuals that may not have oviposited. Gersdorf (1955) indicates that in Germany, where oviposition usually starts about October 4, he found practically no green peach aphid eggs when there was a severe drop in temperature by October 10.

Parasitization must also influence the number of eggs deposited. Parasites in the larval stage were taken from oviparous adults of the potato aphid at three out of the eight stations where collections were made on swamp rose, and from green peach aphids collected on two occasions at one of the four stations on Canada plum. Although solitary parasitic larvae were usually found, at one place two were found in each of two potato aphids. Depending upon location, the percent parasitized at any time of collection ranged from 0 to 100 for the potato aphid and from 0 to 14 for the green peach aphid. No mature eggs were found in the six parasitized oviparae examined; in fact, in all but one there were no distinguishable eggs in the ovaries or they were very small. In one parasitized potato aphid two eggs three-fourths grown were found. Concurrent collection and examination of large nymphs of this aphid also revealed the presence of internal parasites in the larval stage in some specimens.

[5] In a communication dated May 17, 1960, Netherlands Research Council, Bennekom.

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Fringe Populations of the European Corn Borer, *Pyrausta nubilalis*: Their Characteristics and Problems[1]

H. C. CHIANG[2]

ABSTRACT

The distribution of animals is often limited or isolated into populations. Whenever a population has a boundary, there exist fringes. Five major types of population fringes —climatic, topographic, biotic, advancing, and artificial —are briefly discussed. The Minnesota and South Dakota populations of the European corn borer show a climatic fringe in the north, and an advancing and a topographic fringes in the west. The characteristics of the three types of fringe populations are described, and the practical difficulties in insecticidal control of this insect that resulted from the fringe characteristics are considered. More knowledge on fringe populations is needed and would be valuable in practical fields such as game and fishery biology and biological and chemical control of insects. It also may elucidate the basic ecological principles involved in the natural control of animal populations, and in the adaptive variation and hybridization among animal populations.

The concept is fairly well accepted that within the range of a species two areas should be recognized, the main area and the fringe area. The population in the fringe area has been called the "fringe population" by some, and "marginal population" and "periphery population" by others. The relation between main area and fringe area is shown schematically in figure 1. The fringe of the range may be of different widths, and in the diagram the fringe area is greatly exaggerated in relation to the size of the main area. The term "front" is used to indicate the outside edge of the range. Conceivably, when a population expands and recedes the front will shift back and forth.

In the field of ecology, a great deal of attention has been given to the distribution and abundance of animals and the factors affecting them. Only recently some attention is being given to the structure of the population in fringe areas. Townsend (1952) showed that there is a difference in the chromosomal constitutions of the fringe population and of the main population of *Drosophila willistoni*. Carson (1955) in discussing the distribution of American elm (*Ulmus americana L.*), recognized two types of marginal populations of this species; static and dynamic. The present author believes that since the range of the distribution of an animal is usually delimited by forces from without, or barriers, and since the fringe population is exposed more directly to these forces than is the main population, there would be as many types of fringe populations as there are types of barriers.

In the present paper, first we will categorize, on a theoretical basis, the different types of fringe populations, most of which are related to the types of barriers which delimit the distribution. Then we will present the examples shown by the European corn borer, *Pyrausta nubilalis* (Hbn.), in Minnesota and the neighboring state of South Dakota. The characteristics of the fringe populations of this insect and the resulting practical problems in controlling it will be discussed. It is hoped that this discussion will stimulate more studies on this aspect of population ecology.

TYPES OF FRINGE POPULATIONS

1. *Climatic Fringe Populations.*—The distribution of many animal species is limited by unsuitable climatic conditions. These conditions may be as dominant as a low annual rainfall, a low annual mean temperature, or extreme annual or daily temperature fluctuations. They may also be as brief as a few days' low minimum temperature during the winter or even during the summer. This type of fringe is perhaps the most common. The changes in climatic conditions across a vast area are usually rather gradual. As a result, the fringe population of this type may occur in a zone of varying widths.

2. *Topographic Fringe Populations.*—The range of

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[2] Department of Biology, University of Minnesota, Duluth 11, and Department of Entomology and Economic Zoology, University of Minnesota, St. Paul 1.

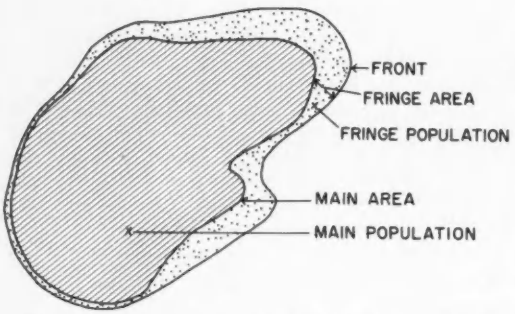

FIG. 1.—Schematic diagram of the main area and the fringe area in the range of distribution.

some animal species is limited by topographic features. A mountain range is a topographic barrier. It also may result in drastic differences in the climatic conditions on the two sides of the barrier. A river, however, which is capable of stopping the expansion of the distribution of certain animal species, may not affect the general climatic conditions. Thus, the fringe populations near a mountain may also show the characteristics of climatic fringe populations, whereas the fringe populations at a river may be strictly topographic.

3. *Biotic Fringe Populations.*—All metazoa depend, directly or indirectly, on vegetation. The lack or paucity of suitable vegetation will result in a population fringe. Vegetation, like animals, will spread until stopped by forces from without, climatic or topographic. Thus, the characteristics of the fringe population of the animal which depends on a particular vegetation will be influenced by the type of fringe shown by the latter.

A variation is conceivable. An animal may at first be limited by the distribution of its food plant. But this animal may become adapted to a new food plant which has a wider range than the original species. When this happens, the original fringe will dissolve into a new phase of expansion. The eastward expansion of the range of the Colorado potato beetle offers an example of this situation (Elton 1958).

A further variation may be noted where human effort is involved. The distribution of plants, particularly those of economic importance, has been extended by human efforts. Breeding of hardy plant varieties and irrigation in arid areas have extended the distribution of some plants into areas which formerly had been too cold or too dry. In such cases, the animal-dependents may be biologically incapable of following immediately the new expansion of the range of the host plants. Then the fringe of the range of the animal species could not coincide with that of the host plants. However, if the animal could have survived the physical conditions beyond its range had the distribution of the host plant not been the limiting factor, then the animal-dependent would be expected to follow the new expansion of the host plants.

Another type of biotic fringe has resulted from the presence of natural enemies. Disease-transmitting insects have, for centuries, prevented human beings from inhabiting certain areas of the globe (Chandler 1944). In this case, the fringe of human populations dovetailed with that of the populations of the insect-pathogen complex. The latter populations are limited most likely by climatic factors.

4. *Advancing Fringe Populations.*—The fringes of the ranges of most of the native animals are geographically stabilized within wider or narrower zones. Theoretically, however, the range of these species must have, during the past ages, gone through stages of expansion and showed fringes which were continuously advancing before it was stopped by forces from without. The location of this type of fringe will be a function only of the intrinsic factors of the species and of time. Probably many indigenous species are still in the process of active expansion, such as some tsetse-fly populations. However, actively advancing fringes among the present-day species may be found most readily under certain circumstances resulting from human actions, as will be discussed presently.

5. *Artificial Fringe Population.*—The fringe of the range of many species is influenced directly or indirectly by human actions. Some fringes are advancing (as mentioned in the preceding paragraph) or receding; others are stable.

The artificial advancing fringes may be shown by populations (a) which have recently established in a new territory through intentional or unintentional human efforts, or (b) whose barrier has recently been removed by human actions. A moving fringe may also be receding. This may be observed among species pressed by artificial control measures or by changes of habitats resulting from soil or water management.

The range of a species may be kept stable by artificial barriers. One such barrier is the quarantine practices against injurious insects. If the quarantine is effective, the range of the species may be stabilized. Domestic quarantine, however, usually also involves an intensive control program to decrease the population density. In this case, the range of the species may even be caused to recede; this results in a receding fringe population as mentioned earlier.

A second type of artificially stabilized fringe is the result of a change in vegetation, particularly a direct elimination of a food plant. If the elimination were incomplete, and if there were heterogeneous regeneration of the vegetation, more marked population fluctuations as well as a greater abundance of life may be found in the fringe areas than in the main part of the distribution (Audy 1948).

EUROPEAN CORN BORER POPULATIONS IN MINNESOTA AND SOUTH DAKOTA

1. *A Brief History of the Establishment and Spread of the Insect.*—The European corn borer was first found in Massachusetts in 1917. It gradually spread westward, and in 1921 it was found along the

southern shore of Lake Erie. The spread then became predominantly southward and westward to flank the great lakes (Everett et al. 1958). The insect was first found in Minnesota in the southeast corner in 1943 (Anonymous 1952). After the borer became abundant in Iowa, invasions of moths into Minnesota from points directly south probably also took place. Thus the expansion of the borer distribution in Minnesota was both westward and northward. The borer abundance in Minnesota has fluctuated a great deal. As of now (and this has been the case for some time) the northward spread seems to have

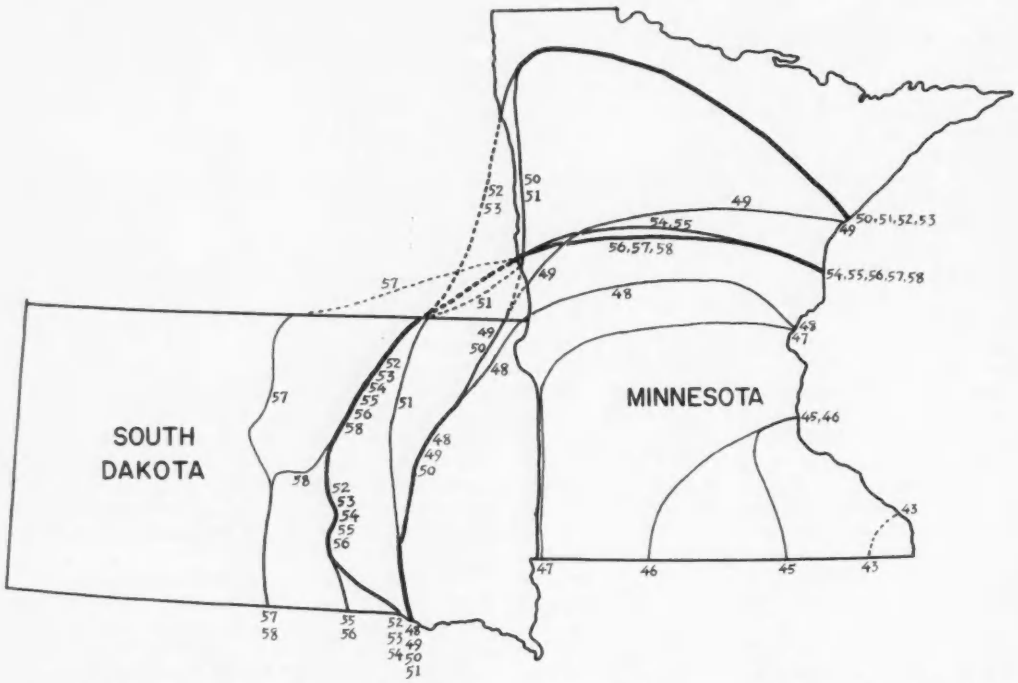

FIG. 2.—Yearly changes of distribution of the European corn borer in Minnesota and South Dakota. The lines represent the west and north fronts of distribution.

stopped and a somewhat definite fringe may be noted just north of central Minnesota. The westward spread, however, swept across the width of Minnesota and reached the Dakotas. This spread was stopped temporarily at the Missouri River in central South Dakota, but now the insect has crossed the river. The yearly changes in the distribution of corn borer in Minnesota and South Dakota since 1945 are shown in figure 2.

2. *Life Cycle of the Corn Borer in Minnesota.*—The insect overwinters as a mature larva. It pupates in late May and early June, and moths emerge shortly after. The moths lay eggs on the leaves of corn plants in June and early July. The larvae hatch within a week after the eggs are deposited, and feed on the leaf tissues. In late July, they reach the third or fourth instar and then bore into the stalk of the plant. A varying proportion of these larvae reach maturity in late July or early August, and then pupate. The remaining larvae stay as larvae throughout the summer and the fall. Those that pupate emerge as adults in August. These moths deposit eggs which initiate the second brood of the annual life cycle. The second-brood larvae feed on various tissues of the plant and then enter the stalks at an earlier stage than the first-brood larvae. Various proportions of these larvae reach maturity in the fall. These mature larvae and those from the first brood make up the overwintering population. Those larvae perish that do not reach maturity before killing frosts occur.

3. *Fourteen-year Survey Records of Borer Populations.*—The Minnesota Department of Agriculture, Dairy and Foods (1948 to 1958) has made surveys of borer populations since 1945, and the South Dakota Agricultural Experiment Station since 1948 (Spawn 1952). The borer populations were expressed in the published reports as the average number of larvae per 100 plants in a given county in the fall.

We are concerned in this discussion with the fringe populations. As we have mentioned, the spread of this insect in Minnesota was mainly in two directions, westward and northward. Thus, results of the popu-

lation density will be presented only insofar as they elucidate the characteristics of the population spread and of the fringe populations. Two transects were made from the original source of population (southeast corner of Minnesota) to the west and to the northwest (figure 3). The yearly records of the populations along the two transects are presented in figures 4 and 5. The two counties with the highest population densities along the transect in a given year are indicated by shading. The counties with no numbers are those either with no borers or where the borer population was extremely low. For practical purposes, the most northern (in figure 4) and the most western (in figure 5) counties which have numbers represent the fronts of the spread.

CHARACTERISTICS OF THE FRINGE POPULATIONS OF CORN BORER

1. *Population at the Northern Fringe.*—From 1945 through 1952, the distribution of corn borer has expanded about 400 miles into Minnesota. Since 1952, however, it has receded appreciably (figure 4). The following facts may be noted regarding the characteristics of the population at the northern fringe: (1) The highest population densities on the entire transect in different years varied greatly during the 14-year period. (2) The population density at a given locality also varied greatly during this period. (3) Throughout the transect, the populations were very low in most counties and in most years. (4) While the front of the population spread advanced and receded for about 200 miles, the majority of the loci of the high population densities shifted within a narrower zone. (5) In all years, excepting 1951 and 1958, the loci of high population densities were located some considerable distance behind the front of the population spread. The above facts suggest that the borer population observed has reached the limit of its distribution and has been stopped by extrinsic factors. Thus, the borer population in Minnesota may be considered as a fringe population occupying a zone whose width has varied greatly during the 14-year period. This consideration is reasonable in view of the vast areas south of Minnesota that are occupied by the borers, and the generally consistently higher densities of populations south of Minnesota.

Chiang and Hodson (1959b) have suggested that this fringe is the result of harsh climatic conditions, including heavy rains and winds, low summer temperatures, and early frosts. The frequent occurrence

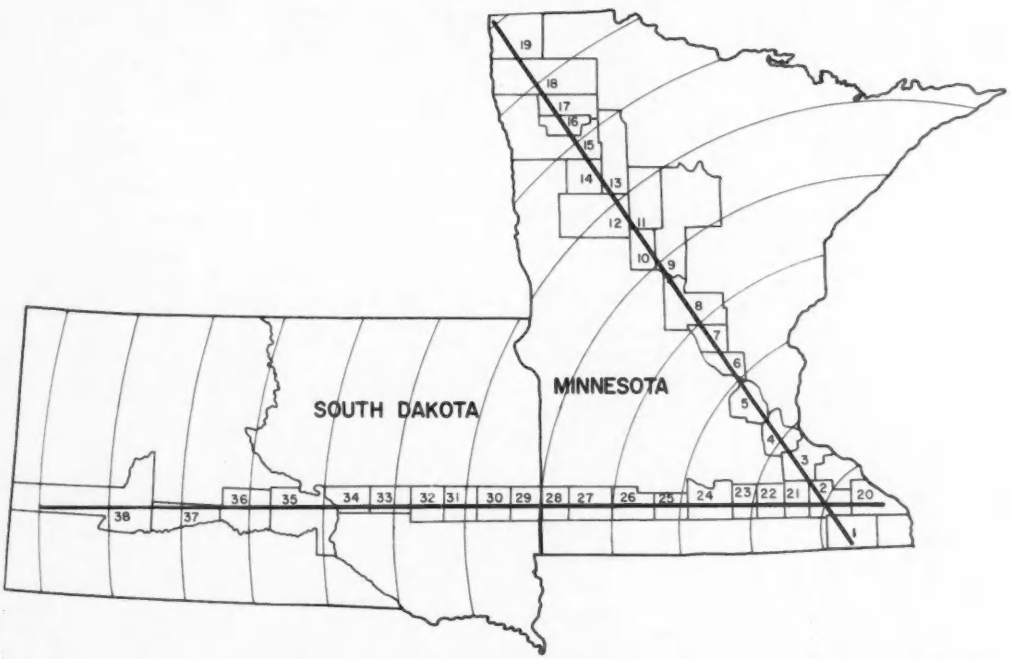

FIG. 3.—The two transects through Minnesota and South Dakota. The borer populations in the counties along these transects are discussed in this paper. The numbers for the counties correspond to those in Figures 3 and 4. The concentric rings indicate 50-mile distances. The counties are: 1. Fillmore, 2. Olmstead, 3. Goodhue, 4. Dakota, 5. Hennepin, 6. Sherburne, 7. Benton, 8. Morrison, 9. Cass, 10. Wadena, 11. Hubbard, 12. Becker, 13. Clearwater, 14. Mannomen, 15. Polk, 16. Red Lake, 17. Pennington, 18. Marshall, 19. Kittson, 20. Winona, 21. Dodge, 22. Steel, 23. Waseca, 24. Blue Earth, 25. Watonwan, 26. Cottonwood, 27. Murray, 28. Pipestone (1-28 in Minnesota), 29. Moody, 30. Lake, 31. Miner, 32. Sanborn, 33. Jerauld, 34. Buffalo, 35. Lyman, 36. Jone, 37. Jackson, 38. Pennington (29-38 in South Dakota).

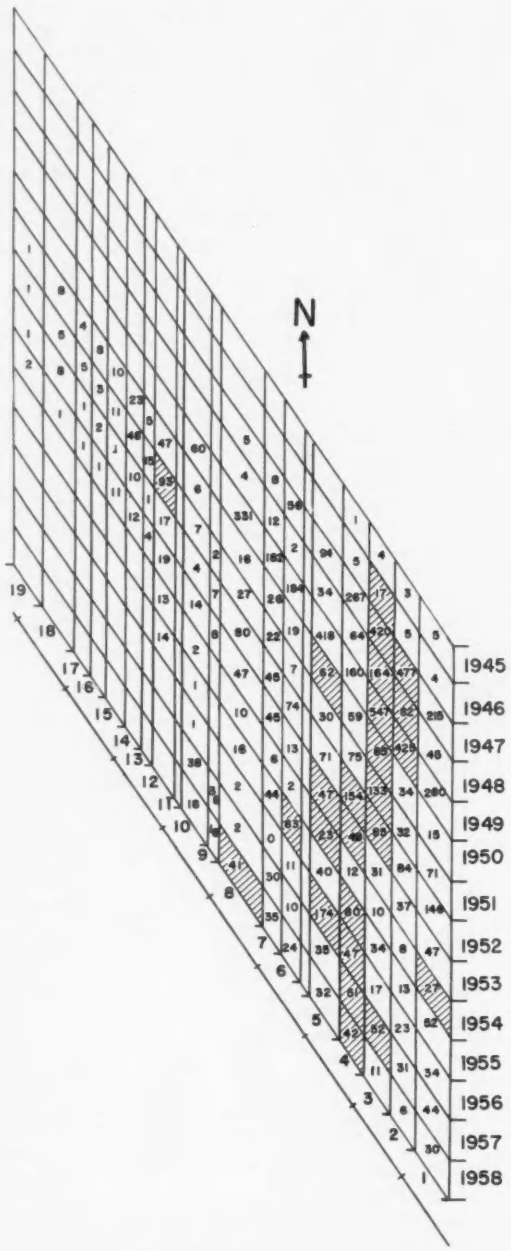

FIG. 4.—The population changes during the 14-year period, 1945 to 1958, in the counties along the SE-NW transect. The number indicates the number of borers per 100 plants in the fall. The counties with the highest populations for a given year are shaded. Counties and years with no number were not surveyed because the borer population was either absent or too low to get any significant data. The base line marks the 50-mile distances.

and the variable combinations of these factors are responsible for the generally low population levels and the haphazard fluctuations of borer population in the fringe areas. Quite definitely the northern fringe of borer distribution is not limited by the availability of host plants, since corn is planted in areas beyond and much north of the borer fringe. A speculative remark may be offered in this regard. The presence of significant acreage of corn in the more northerly areas is the result of breeding programs which produced quicker-maturing and more hardy varieties (Wallace and Bressman 1949). Thus it is logical to assume that artificial means have extended the fringe of corn populations into areas normally too cold for the plant. The fringe of borer populations, on the other hand, remained behind because the insect is limited by its own degree of tolerance to the physical elements. Reference should be made to the second variation under the Biotic Fringe discussed earlier.

2. *Population at the Western Fringe.*—During the same 14-year period, the borer population has spread about 400 miles across Minnesota and into South Dakota. The following facts are shown in its westward spread. (1) The westerly spread was continuous, without any recession. (2) The borer population has spread the same distance toward the west as its maximum spread toward the north. (3) The rate of spread was higher in the early years (1945-1948) than in the later years. The spread was stopped from 1952 to 1956 at the Missouri River, but the insect has since crossed the barrier. (4) The loci of the highest population densities from 1945 through 1952 did not shift as they did at the northern fringe. Instead, they moved continuously westward with the population spread. As an analogy, one may visualize the progress of a ring of swell on the water surface starting at the point of impact of a piece of rock. (5) From 1952 on, coinciding with the cessation of the spread, the loci of the highest population densities shifted back and forth, although in the main they were still quite near the front of the spread. (6) The average as well as the peak population densities were higher in the western fringe than in the northern fringe. This was true in 12 out of 13 years.

During the 14-year period, two types of fringes were shown at the west front: an actively advancing fringe, and a topographic fringe. From 1945 to 1952, the population spread with great speed from the east edge of Minnesota to the Missouri River in central South Dakota. This movement was continuous and apparently encountered no hindrance forces from without, since along the path there were no major changes in host availability or climatic conditions, nor were there any topographic barriers. Thus, the fringe during these years represented an active and advancing fringe (see type 4 in the first section of this paper).

From 1953 to 1956, the spread was stopped abruptly by a topographic factor but there was no recession of the fringe. The loci of the peak populations stayed

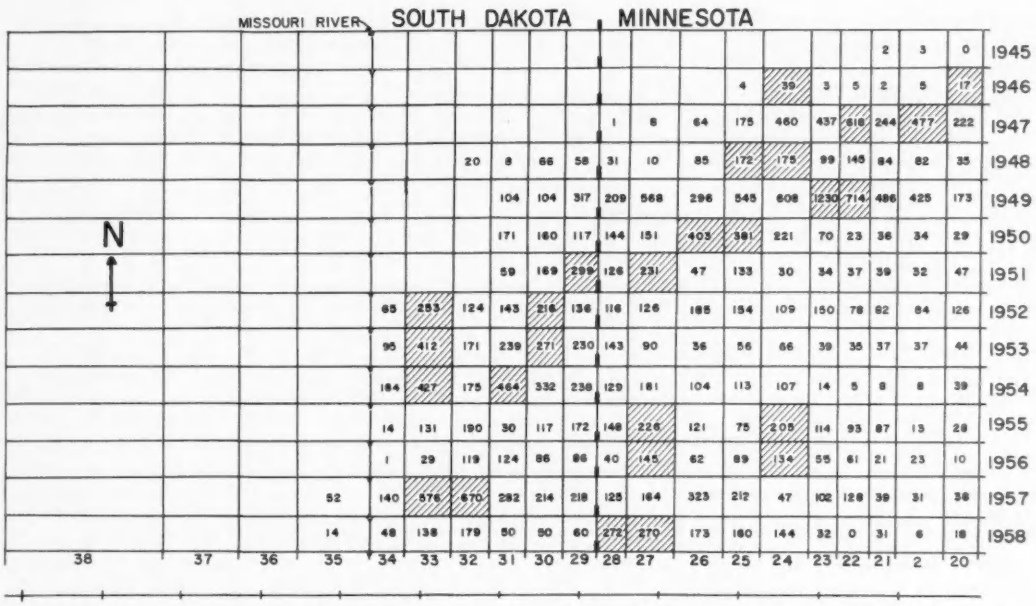

FIG. 5.—The population changes during the 14-year period, 1945 to 1958, in the counties along the E-W transect through Minnesota and South Dakota. The number indicates the number of borers per 100 plants in the fall. The counties with the highest populations for a given year are shaded. Counties and years with no number were not surveyed because the borer population was either absent or too low to get any significant data. The base line marks the 50 mile distances.

near the front of the spread for three years, and then began to shift back and forth. These phenomena were very different from what was found at the climatic fringe in the north, and may thus be considered characteristic of one type (river) of topographic fringe.

The population west of Missouri River may resume an active expansion. There are, however, some observations which suggest that the borer population may soon meet another climatic barrier in western South Dakota. Corn is grown abundantly in the irrigated areas in western S. D., but only negligible borer populations have been observed there even after the borer crossed the river.[3]

3. *Comparisons of the Three Types of Fringes.*—The previous paragraphs pointed out that in the north there is a climatic fringe and in the west there was an active advancing fringe (1945 to 1952), and a succeeding topographic fringe (1952 to 1956). The characteristics of the three types of fringe populations as shown by the corn borer in Minnesota and South Dakota are now summarized as follows: (1) In all the fringe areas the population density was generally low in most of the years, but showed sporadic peaks. (2) In all the three types of fringes observed, the population density at or near the front was higher than that of the original source, namely the southeast corner of Minnesota. (3) The spread of the population is stopped more abruptly on meeting a topographic barrier, such as a river, than on approaching a climatic limit. This is perhaps to be expected since the change in climatic factors is gradual and variable while the demarcation of a physical barrier such as a river is clear cut. (4) The loci of the highest population densities stayed relatively stationary and at a considerable distance from the front in the case of the climatic fringe, but moved continuously with, and immediate behind, the front of population spread in the case of an active and advancing fringe. (5) The average as well as the peak population densities in the western fringe was higher than those in the northern fringe. (6) The mechanisms which brought about these characteristics are yet unknown. Studies on this subject would undoubtedly be very valuable and fruitful.

4. *Speculations on Possible Mechanisms of Fringe Characteristics*—Little is known about the characteristics of fringe populations as mentioned in the preceding paragraphs. The most puzzling is perhaps the "swell" phenomenon, i.e., the presence of peak populations near the front of the spread. This phenomenon appears contradictory to the negative logarithmic relationship between the population density and the distance of dispersal from the population source. The latter relationship has been shown in numerous organisms, as reviewed by Wolfenbarger (1946).

Continued studies on the fringe characteristics

[3] Personal correspondence with William Hansbarger, Extension Entomologist, South Dakota State College.

would undoubtedly be valuable and fruitful. For further investigations, the following hypotheses are proposed for testing.

(1) *Differential intrinsic vitality.*—Wellington (1957) demonstrated the individual differences among the larvae and adults of the western tent caterpillar, *Malacosoma pluviale* (Dyar), regarding their activity. He observed that (a) colonies in new infestation consisted largely of active larvae, whereas less active larvae occurred with increasing frequency as infestations became older and heavier, and (b) more active moths appeared to be responsible for production of active colonies, especially in new infestations most distant from original sources. This biological phenomenon could be present also among the corn borer populations. If so, one might expect the population densities at or near the front to be higher than those elsewhere.

(a) *Differential reproduction due to exercise.*—Johnson (1958) demonstrated that bodily exercise is essential for normal reproduction in the bean aphid, *Aphis fabae*. If this effect of bodily exercise exists also in the corn borer, one might expect that those moths which invaded a new territory would have had more bodily exercise (through flight) than those that remained behind. Consequently, moths near the front would be more prolific and might contribute to a higher population there.

(3) *Differential speeds of spread of the corn borer and its natural enemies.*—If the mobility of corn borer is higher than that of its host-specific enemies, there would be a zone near the front of the spread in which the borer enjoys a higher survival.

ADAPTIVE FEATURES OF FRINGE POPULATIONS OF CORN BORER

As shown in figure 4, the northern fringe of the corn borer population has been subjected to great expansions and recessions but the loci of the highest population densities have shifted within a relatively narrow range. Nevertheless, the densisty at a given locality throughout the 14-year period fluctuated greatly. It has been suggested that haphazard weather changes, however momentary some of them might be, could sufficiently explain such fluctuations. Thus violent fluctuations may be considered one of the characteristics of fringe populations.

Of whatever genetical origin, the borer shows certain adaptive features which clearly manifested their value in the survival of this species under the climatic conditions prevailing in Minnesota. In other words, without these adaptive features, the northern fringe might have occurred much further south of where it is now.

1. *Winter Hardiness.*—Minnesota, particularly areas north of the extreme southern part of the state, compared to the main corn belt, has (1) lower mean summer temperatures, (2) earlier frosts, and (3) more severe winters. The severe winter in Minnesota is considered the primary factor in preventing many insects from overwintering and establishing in the area. For the corn borer, however, the low minimum temperatures in the winter are perhaps of least significance of the three factors, because of the ability of the borers to survive extremely low temperatures. Barnes and Hodson (1956) showed that the mature larvae which acquired cold hardiness survived the entire winter in the field with their body in a frozen state.

2. *Bivoltinism.*—As mentioned earlier, in Minnesota varying percentages of the mature larvae pupate in the summer and produce a second brood, and varying proportions of the second-brood larvae reach maturity and enlarge the overwintering populations. Chiang and Hodson (1959b) observed that a population of summer mature larvae of a given size may result in an overwintering population many times as large as, or only a fraction of, the summer population. However, if frosts came early, the entire population of the second-brood larvae may be killed. In such years, the higher the percentage of summer pupation, the smaller would be the overwintering population. Thus, in some years, summer pupation and the presence of a second brood may work a great disadvantage to the survival of the borer populations. Throughout a 10-year period, however, the population was actually kept at a higher average level than if the insect has a univoltine life cycle.

Some data presented by Chiang and Hodson (1959b) of the population changes in one field each year for a period of 10 years (1948-1957) in Waseca County, Minnesota, are analyzed on a theoretical basis to clarify the above point. The number of mature larvae in the summer and in the fall are given in table 1, rows 1 and 2. The ratio, either an increase or a decrease, of the fall population of one year and the summer population of the following year was calculated as shown in row 3. This value represents the over-all success of a succession of events: winter survival, spring pupation, moth emergence, egg deposition, larval hatching and larval survival, for a given year. If the borers were univoltine, there would be no pupation during the summer, and the entire population in one summer would go into hibernation, and then pupate and emerge as moths which produce the first-brood (or the only brood) population in the second summer. Now let us assume further that these hypothetical overwintering larvae would have the same degree of success in producing the mature larval population in the following summer as did the actual overwintering larvae. On these bases, the number of mature larvae expected in the second summer could then be computed; this number is given in row 4. Then the computed number of mature larvae in the second summer, instead of the actual number of mature larvae present, will be used for computing the expected number of mature borers in the third summer. Thus, the numbers in row 4 represent the theoretical population densities throughout the 10-year period if the borer had been univoltine. The calculated densities of a theoretical univoltine population are graphed along with the

Table 1.—Comparison of the densities of the corn borer populations at Waseca, Minnesota, from 1948 to 1957 as recorded by Chiang and Hodson, and as calculated on the hypothetical basis of one generation yearly.

Year	Observed number of larvae[a] that matured in		Ratio of summer larvae of given year to fall larvae of preceding year[b]	No. of mature larvae[a] expected on hypothetical basis of one generation per year[c]
	Summer	Fall		
1948	57	111	——	[57]
1949	150	147	1.35	77.0[d]
1950	434	410	2.9	223.3
1951	135	122	0.33	74.9
1952	41	59	0.34	25.5
1953	39	39	0.66	16.8
1954	21	13	0.54	9.1
1955	0[e]	16	0.1	0.9
1956	28	18	1.7	1.5
1957	7	—	0.39	0.6

[a] Per 100 plants.
[b] Examples: 150/111 = 1.35; 434/147 = 2.9; etc.
[c] That is, if the preceding year's summer generation had continued until fall without pupating and had undergone hibernation.
[d] Examples: 1.35 × 57 = 77.0; 2.9 × 77 = 223.3; etc.
[e] In 1955 no first-generation egg masses or larvae were found on those plants that were marked for study, but a few were found elsewhere in the same field. The value of the ratio for this year in column 3 is arbitrarily set at 0.1.

actual densities of the bivoltine borer population in figure 6. If the assumptions were sound, this comparison will indicate that throughout the 10-year period, the borer density has been maintained at a higher average than if the borer did not have a second brood. Thus, it may be suggested that even though bivoltinism has caused losses in population in some individual years, it is an adaptive feature of value in the long range population growth in the northern fringe.

PRACTICAL PROBLEMS IN THE CONTROL OF FRINGE BORER POPULATIONS IN MINNESOTA

At their northern fringes, the borer populations in Minnesota showed haphazard fluctuations in respect of both time and magnitude. But the average population density in general throughout a 14-year period was low. These characteristics of fringe populations have presented some problems in the insecticidal control program of this insect.

Many farmers in Minnesota are not very much impressed by the corn borer damage that they have seen, excepting in the years 1947, 1949, and 1950. Consequently, they do not see any urgent need to do anything about control. This situation is due not only to the nature of borer damage, but also to the generally low population densities. The success of the insecticidal control of this insect depends a great deal upon the ability of farmers to identify and count the egg masses. Some years ago, six farmers, selected from among the best informed in Waseca County, Minnesota, were tested for their ability to count corn-borer egg masses.[4] The results of the test were very disappointing. Some irrelevant objects were counted as egg masses and many egg masses were unnoticed. The number of egg masses found by farmers was not at all close to the number actually present. The deviation was so great and so variable that it was impossible even to try to correct their figures with a correction factor. This poor performance was partly the result of the difficult skill involved in identifying the egg masses, particularly the hatched ones. Just as significant, however, was the fact that the farmers had little need and little opportunity to acquire this skill, owing to the low population levels during most of the years. Many farmers in the area, in fact, considered borer infestation as just one of the natural hazards of farming, along with hail and windstorms. This situation, however discouraging it may be to the entomologists, is due more to the circumstances inherent in a fringe population than to any real incompetence of the farmers.

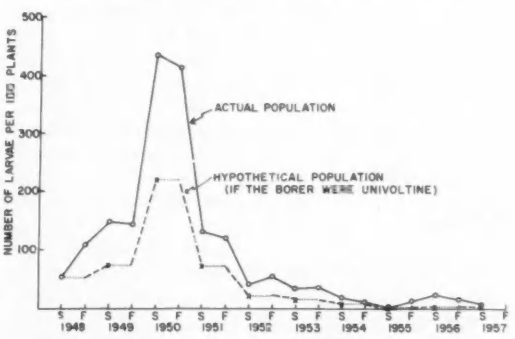
NUMBER OF LARVAE PER 100 PLANTS
500
400
300
200
100
ACTUAL POPULATION
HYPOTHETICAL POPULATION
(IF THE BORER WERE UNIVOLTINE)
S F S F S F S F S F S F S F S F S F S F
1948 1949 1950 1951 1952 1953 1954 1955 1956 1957

FIG. 6.—Comparisons of the populations as reported by Chiang and Hodson (1959b) which are bivoltine and the populations calculated on a theoretical basis on the assumption that the borer is univoltine. "S" summer, and "F" fall.

[4] *See:* A critique on some aspects of the corn borer control program for field corn in Minnesota. Unnumbered circular, Department of Entomology and Economic Zoology, University of Minnesota. 1952.

More recent investigations have revealed that a frequency index of egg masses on plants may be used to determine the population level (Chiang and Hodson 1959a) and that the percentage of plants with injury sites from borer feeding may be used to determine the best time for applying insecticides. (Chiang and Hodson 1953). This information might simplify some aspects of the control procedure, and remedy the present difficult situation.

It is understood that any recommended procedure for crop protection against insect damage should be simple and easy to follow. From the foregoing discussion, this rule clearly is even more critical in dealing with a fringe population, such as that of the corn borer, than with others.

MORE KNOWLEDGE ON FRINGE POPULATIONS

We have classified the possible types of fringe populations and characterized three of these which are shown by the corn borer. Recognizing that the borer populations in Minnesota are fringe populations, and knowing the characteristics of such fringe populations, have brought us to realize that some of the difficulties in the control program are inherent in fringe populations. To face the situation squarely, simplified procedures were developed which, it is hoped, would be more practicable. However, as mentioned before, much work is still needed to investigate the mechanisms which brought about the fringe characteristics.

The solution of other practical problems in population ecology may also be facilitated by a greater knowledge of fringe populations. Game and fishery biologists sometimes are concerned with the extension of the natural ranges of game and fish species. Such extended establishments may show different characteristics merely because they constitute fringe populations. Entomologists engaged in biological control of insects may face the same situation when they introduce natural enemies into a new territory. A knowledge of the characteristics of the fringe populations of the species concerned in their native land will perhaps be valuable in such tasks. Furthermore, new methods of insect control, such as synthetic organic insecticides and male sterilization by irradiation, have revived the hopes for eradicating certain insect pests, such as the gypsy moth and the screwworm. Such programs are usually designed to begin at the fringe. Knowledge of the characteristics of fringe populations of such species will be valuable in planning the control procedures and in evaluating the results.

Fringe populations deserve special attention also from a basic ecological viewpoint. The relative importance of density-dependent factors and density-independent factors in the natural control of animal populations has been a much discussed, controversial question. Failure to recognize the existence of fringe populations, and the lack of information of the characteristics of such populations may lead to a wide difference in interpretation of results. Such a difference is bound to occur when results of a field population which happens to be in a fringe area, are compared with those of a laboratory population, which seldom, if ever, shows fringe characteristics. In this connection, something might be learned in the laboratory regarding the characteristics of fringe populations by exposing the test animals to harsh and marginal conditions, in addition to the conventional optimal conditions.

Another aspect is related to the genetics and evolution of the species. Climatic fringe populations are under harsh physical conditions. The selection pressure is usually strong. As a result, adaptive variations may manifest themselves more quickly. In a study of the genetic characteristics of *Drosophila robusta*, Carson (1955) concluded that central populations are less likely to foster the formation of major adaptive novelties than are marginal populations of the same species. Moreover, if two species overlap in their ranges, the species would show the greatest amount of mixing at the fringes. As a result, the fringe populations would have a greater chance for hybridization than would populations in the main area of distribution. This phenomenon has been shown in the pigweeds (genus *Amaranthus*) by Sauer (1957), who observed that with geographic expansion, former limited overlap between species of this genus has greatly widened and exceptional hybridization has become common. Hence, the studies of fringe populations would offer excellent opportunities to observe the development of adaptive variation and hybridization, and the effect of such development on the long range population changes.

ACKNOWLEDGEMENTS

Sincere thanks are due to Professors A. C. Hodson and F. G. Holdaway of the Department of Entomology and Economic Zoology, University of Minnesota, and to Professor L. C. Birch, Department of Zoology, University of Sydney, Australia, for reading the manuscript and for their valuable suggestions.

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The Thoracic Musculature of the Indian Rat Flea, *Xenopsylla cheopis* (Siphonaptera)[1]

ROBERT E. LEWIS

American University of Beirut, Beirut, Lebanon

ABSTRACT

The thoracic muscles and their functions are described in supplement to studies by previous workers on the muscles of the siphonapteran head and legs. *X. cheopis* has many fewer thoracic muscles than less specialized insects. The trochanteral depressors, which are the principal extensors of the legs, are relatively of great size. The other surviving muscles act mainly to hold the various parts of the body firmly together. The flea is highly adapted not only to strenuous jumping but also to sinuous creeping among the hairs of its host. The muscular pattern of the flea, though much reduced from the primitive condition, is such as to render a derivation of the fleas from the Coleoptera or Diptera most unlikely. Considering also other structural, physiological, and ecological factors, the bulk of the evidence leans heavily toward the view of Tillyard (1935) that the order Siphonaptera is the offshoot of some primitive mecopteran stock.

Since the turn of the century, due mainly to the incrimination of *Xenopsylla cheopis* (Rothschild) as the primary vector of the Black Plague, fleas have been the subject of considerable study. Although much of this research has dealt with the distribution and taxonomy of the order, a few major publications have been concerned with the anatomy, morphology, and embryology of its species. The investigation of Bacot and Martin (1914) not only demonstrated that the Indian rat flea is the primary vector of the plague, but also showed the mechanics of transmission to be dependent on the internal anatomy of the vector.

The first serious examination of the musculature of the flea was that of Jacobson (1940). This work, although limited to a study of the arrangement and function of the muscles of the legs, including those muscles which extend into the thorax, is quite detailed and thoroughly illustrated.

Six years later, the study of Snodgrass (1946) upon the skeletal anatomy of fleas standardized the interpretation of the various exoskeletal components and provided the basis for a detailed consideration of the muscles found within the group.

The most recent investigation into the anatomy of fleas is that of Wenk (1953). It gives the first full description of the composition and function of the muscles of the head, and is particularly pertinent to the present study since it treats also the muscles of the cervical region, most of which find their origin or insertion with the thorax.

The Siphonaptera is one of the few orders in which thoracic musculature has never been described. The information reported here should therefore be useful for comparative purposes, as well as for its bearing on the function of these muscles in the flea and for the inferences it suggests as to the manner in which the muscular system of this group has become adapted to a very special mode of life.

MATERIALS AND METHODS

Four types of technique have been employed. The most satisfactory was the use of serial sections cut in transverse, sagittal, and frontal planes. Since mature fleas become very brittle if exposed to organic solvents after the cuticle has tanned, specimens were taken which were physically mature, but whose cuticle had not yet tanned and which had not left the cocoon.

The process of tanning and hardening normally

[1] A portion of a thesis presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Illinois, Urbana, Illinois. Accepted for publication September 19, 1960.

requires approximately 6 hours, while the average duration of pupal life at 80% R.H. and 80° F. was about 9.5 days. Accordingly, fleas which were known to have pupated within a 24-hour period were separated from the culture for 228 hours. They were then placed in vials and warm fixing fluid was poured over them while they were still in the cocoon.

Because of the large amount of air trapped in the cocoon, and the relative impermeability of the cuticle, a strong fixative was employed. This, a modified Carnoy's fluid, was formulated of equal parts of absolute ethanol, chloroform, and glacial acetic acid. Fixation was complete in 1 to 2 hours.

Specimens for sectioning were selected on the basis of their color, a light brown to the appendages indicating that the tanning process had begun. Standard embedding and sectioning procedures were used, and most of the sections were stained with Carazzi's hematoxylin and an eosin counterstain.

The second technique involved the gross dissection of fixed material. The small size of the specimens made it hard to anchor them for dissection, and even attaching them with adhesive was unsatisfactory, due to the extraordinary toughness of the exoskeleton. The best results were obtained with celloidin. Individuals to be dissected were first allowed to remain in absolute ethanol for 12 to 24 hours. Then a flea was laid gently on the surface of a drop of 10% celloidin in the center of a Syracuse watch glass, before the celloidin could form a surface "skin." Since absolute alcohol is one of the solvents of celloidin, the flea began to sink slowly into the drop. At the appropriate stage of immersion the process was stopped by flooding the preparation with anhydrous chloroform. By allowing the preparation to remain in chloroform during the dissection, the exoskeleton could be chipped away without appreciable damage to the underlying tissues.

Once exposed, the muscles were stained with a weak solution of fast green in 95% ethanol. After an exposure of 1 to 2 minutes, the staining solution was poured off and the preparation was rinsed and again covered with anhydrous chloroform.

The remaining techniques employed polarized light or phase-contrast microscopy. Although both were helpful in the gross aspects of the investigation, neither was as revealing of details as the standard light microscope and serial sections.

THE THORACIC MUSCULATURE

In the following account of the thoracic muscles of *X. cheopis*, the sequence and the names of the major subdivisions follow those of Snodgrass (1935). A continuation of the numbering system initiated by Wenk (1953) results in the application of numeral 21 to the first muscle found in the cervical region, which will be described before the thoracic muscles proper.

Cervical Muscles (No. 21; not figured).

The paired cervical muscles of *X. cheopis* correspond to those described by Wenk (1953) for *Ctenocephalides canis*; each consists of two major branches. Both branches have a common origin on the caudal extremity of the cervical sclerite. The dorsal branch (Wenk: *cervicalis exterior*, No. 21a) is inserted on the median crest of the postocciput. The other branch (Wenk: *cervicalis interior*, No. 21b) is attached to the wall of the postocciput slightly laterocaudad of No. 21a.

Both portions are rather small, and the muscle obviously does not play a very important role in the movement of the head. At best, their contraction may cause the head to tilt upward slightly; but, since the head is associated so intimately with the prothorax, little space for such movement remains.

Dorsal Thoracic Muscles

Longitudinal Muscles:

a. *Prothorax* (No. 22, fig. 1). A medium-sized, apparently unpaired bundle arises on the first phragma (1 Ph) and extends cephalad to attach on the postocciput (Poc) dorsal of the tentorial bridge (TB). A slight keel is present on the postocciput, and it is upon this keel that the muscle is inserted.

b. *Mesothorax* (No. 25, fig. 4). In the mesothorax is a large, fan-shaped bundle, paired caudally but fused cephalically. It arises on the ventromesal lips of the second phragma (2Ph) and extends to the first phragma (1Ph), the complete caudal surface of which it occupies.

c. *Metathorax* (No. 26, fig. 2). The longitudinal median dorsal muscle of the metathorax stretches from its origin upon the anterior inflection of the first abdominal tergum (I T) to its insertion upon the caudal face of the second phragma (2 Ph). This is a relatively thin, flattened sheet of muscle which, in cross section, is seen to have thickened margins. It is unpaired, but doubtless is the result of fusion of a pair of muscles.

Oblique Lateral Muscles.

a. *Prothorax* (No. 27, fig. 1). Each member of this pair is a medium-sized bundle which extends posteriorly and ventrally from its origin on the first thoracic notum (N_1) to its insertion on the first phragma (1Ph) near the dorsal margin, in the region of the attachment of the longitudinal dorsal muscle (No. 22).

b. *Mesothorax* (No. 28, fig. 4). The muscles of this pair arise on the meson of the mesothoracic notum (N_2) and extend caudad and ventrad to their respective insertions on the lateral margins of the second phragma (2Ph).

c. *Metathorax*. The oblique lateral dorsal muscles are lacking.

Since the motion of the thoracic segments relative to each other is slight, the principal function of the dorsal muscles is to hold the segments firmly together, as when the body is subjected to the stress of jumping. No doubt these muscles, when used on one side at a time, contribute also to the lateral twisting movements of the flea walking upon its host.

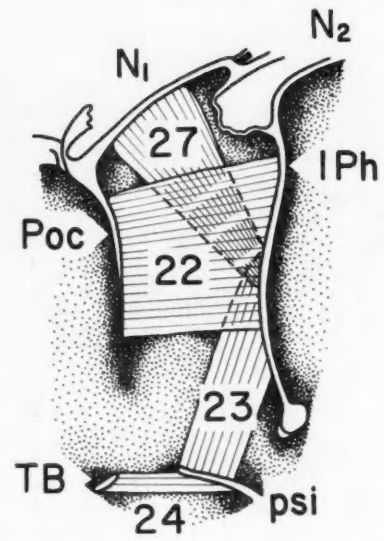

FIG. 1

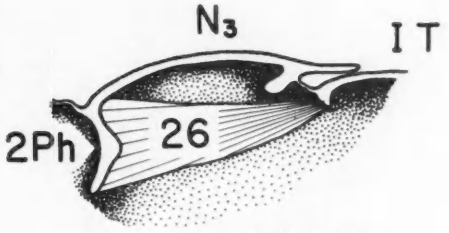

FIG. 2

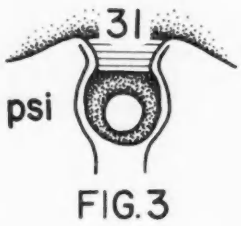

FIG. 3

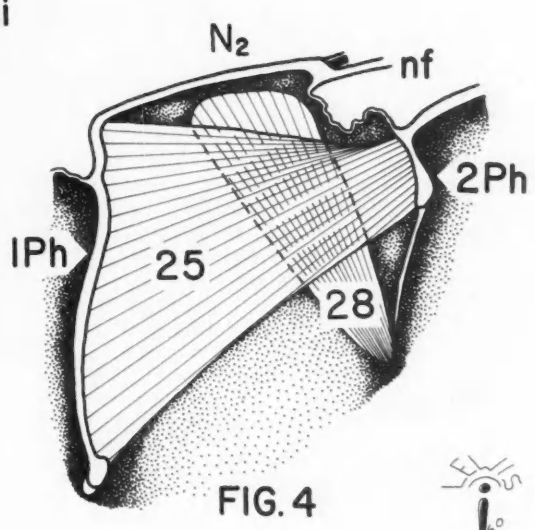

FIG. 4

PLATE 1. *Xenopsylla cheopis*. FIG. 1.—Lateral view of the dorsal longitudinal muscles, the lateral intersegmental muscles, the ventral muscles, and the oblique lateral muscles of the prothorax. FIG. 2.—Lateral view of the dorsal longitudinal muscles of the metathorax. FIG. 3.—Cephalic view of the transverse ventral muscle in the prothorax. FIG. 4.—Lateral view of the dorsal longitudinal muscles and the oblique lateral muscles in the mesothorax.

For key to abbreviations in figures, see page 394

Epipleural Muscles

Although the epipleural muscles are usually associated with the basalare and subalare in winged insects—which are, of course, lacking in the apterous fleas,—there are in *X. cheopis* two pairs of muscles that conceivably would fall into this category.

The first occurs in the mesothorax (No. 38, fig. 7). The muscle originates on the posterior rim of the coxa (cx_2) and extends dorsally to attach upon the ipselateral second link plate (lp_2). The second pair (No. 43, fig. 8) occupies a similar position in the metathorax, but here the dorsal attachment is to the wall of the epimeron (epm_3). There is no link plate between metathorax and abdomen in *Xenopsylla cheopis*. Whether the two groups of muscles are

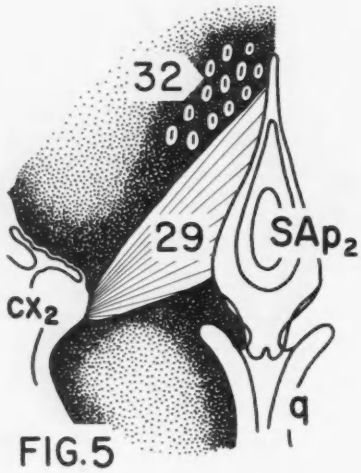

FIG. 5

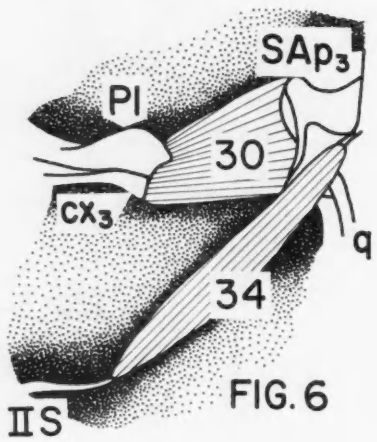

FIG. 6

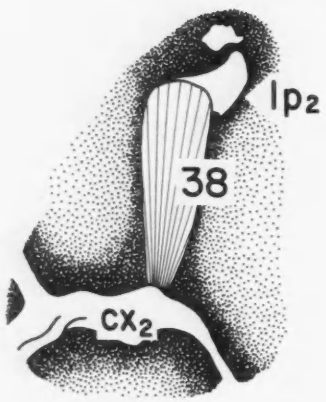

FIG. 7

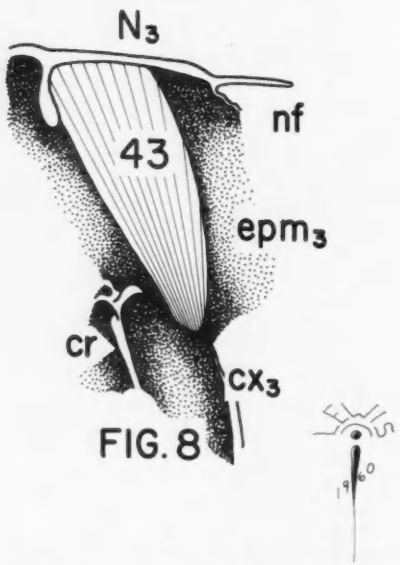

FIG. 8

PLATE 2. *Xenopsylla cheopis.* FIG. 5.—Cephalic view of the pleurosternal muscle and one of the ventral longitudinal muscles of the mesothorax. FIG. 6.—Dorsal view of the pleurosternal muscle and the ventral longitudinal muscles of the metathorax. FIG. 7.—Lateral view of the mesothoracic coxal remotor. FIG. 8.—Lateral view of the metathoracic coxal remotor.

homologous to those epipleural muscles which in other insects extend between the coxa and the subalare is conjectural, although the origin on the posterior coxal rim is suggestive. No muscles were noted which might fit into the "coxa to basalare" group.

The function of the epipleural muscles is discussed below together with that of the sternal muscles of the coxa.

Lateral Intersegmental Muscles

There is only one pair of lateral intersegmental muscles (No. 23, fig. 1) in *X. cheopis.* These extend from the respective attachments on the ventro-

lateral portions of the first phragma (1Ph) to the lateral lobes of the posterior inflection of the prothoracic pleurosternum (psi). Contraction of these muscles increases the integrity of the connection between pro- and mesothorax. Muscle contraction only on one side deflects the head and prothorax in that direction.

Pleurosternal Muscles

The pleurosternal muscles which in most insects extend from the pleural apophysis to the sternal apophysis (*Zwischenmuskel* of German authors) are not represented in *X. cheopis*. There are known to exist also, in some insects, muscles that run from the lower end of the pleural ridge to an attachment upon the sternal apodeme. This type of muscle, although of rare occurrence according to Snodgrass (1935), is present in the meso- and the metathorax of the flea.

The mesothoracic pleurosternal muscles (No. 29, fig. 5) are the larger. They are most readily seen in sections made in the transverse plane. In such sections the pleurosternals are visible as large, fan-shaped muscles that arise upon the pleural articulation of the coxa (cx_2) and expand mesally to occupy the dorsal three-fourths of the mesosternal apodeme (SAp_2).

In the metathorax the pleurosternal muscles (No. 30, fig. 6) are much smaller. Although no conspicuous separation is evident in the insertion, the muscle actually attaches both to the pleural articulation of the coxa (Pl) and to the dorsal lip of the coxa (cx) as well. Relatively few of the fibers are involved in this lower attachment, but some of them extend into the coxa far enough to attach to the coxal rod (cr) at its fusion with the wall of the coxa.

The function of these muscles seems primarily to be that of providing a strong connection between the pleuron and the sternum. The coxal cavity is fairly large, and a muscle extending across it would tend to prevent the points of coxal articulation from being excessively distorted or thrown out of adjustment during the jump. The ventral migration of a portion of this muscle into the metathoracic coxa may be understood similarly, as doing much to ensure the contact of the pleural and coxal points of articulation whenever such intimate contact becomes functionally important.

Ventral Muscles

Since there are no spinisterna in the flea, the ventral musculature is limited (with one exception) to the longitudinal furcal muscles. As compared to the development of ventral muscles in more primitive orders of insects the number of such muscles in *X. cheopis* is drastically reduced. There are four pairs of longitudinal ventral muscles, one of which extends into the abdomen and one into the head, plus one transverse muscle, which is unpaired. Collectively these muscles act, in conjunction with the dorsal longitudinals, further to ensure the integrity of the tagmata and of the several thoracic segments.

a. *Prothorax.* The ventral muscles consist of a single pair of longitudinal bundles (No. 24, fig. 1), which take their origins upon the caudal ridges of the prosternal inflection (psi); and an unpaired bundle (No. 31, fig. 3), which extends transversely between the left and right dorsal extensions of this inflection. The paired muscles course cephalad to points of attachment on the lateroventral margins of the tentorial bridge (TB), which divides the occipital foramen into a dorsal and a ventral passage. They function in opposition to the dorsal longitudinal muscles (No. 22) and the cervical muscles (No. 21), which are the levators of the head. Since, as has already been remarked, the close approximation of the head and the prothorax reduces such movements to a minimum, the more important task of these muscles is the exertion of tension which helps to hold the head firmly in position.

An equally likely explanation is not readily available as to the function of the small bundle of muscle (No. 31, fig. 3) which is stretched transversely across the "trough" in the prosternal inflection (psi). A similarly disposed muscle has been seen only in Mecoptera (Maki 1938; Hasken 1939; Füller 1955; Chadwick, unpublished data), in Mallophaga (Mayer 1954), and possibly as part of the "delicate common net of ventral transverse muscles" in the tipulid fly *Ctenacroscelis* (Maki 1938, p. 244). Such muscles have been interpreted by Chadwick (1959) as having been derived from the fusion of former paired spinafurcal muscles ($lsps\text{-}fu_1$), following loss of the original spinal attachment. Serial homologs with such an arrangement occur in the posterior thoracic segments of a few insects; and, in *Xenopsylla*, the mesothoracic furcal arms are joined across the nerve cord in a skeletal fusion that may have replaced such a former muscular connection between them. Consistent with the view that muscles which are not called upon to function actively may lose their contractile nature and give way to ligamentous or even to sclerous structures (Chadwick 1957), it may be significant that the fibers of this bundle (No. 31) in the flea do not have the banded appearance characteristic of the remaining muscles. The only likely use for this muscle is that of acting as a brace to prevent lateral expansions of the pleurosternum from causing damage; and the muscle may actually be evolving in the direction of becoming ligamentous.

b. *Mesothorax.* Extending caudad from the posterior face of the prosternal inflection (psi) is a pair of muscles (No. 32, fig. 11) which attaches to the winglike lateral processes of the mesosternal apodeme or furca (SAp_2). Contraction of either bundle alone will cause the head and prothorax to be turned slightly in that direction. Thus, these muscles may be regarded as antagonistic to each other. By acting with the remaining intersegmental muscles, they control the lateral deflection of the segments preceding them.

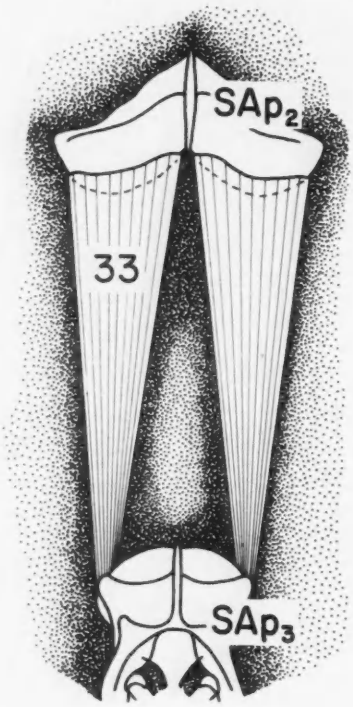

FIG. 9

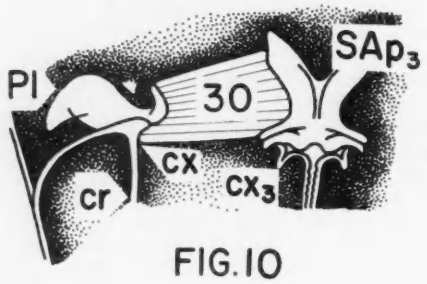

FIG. 10

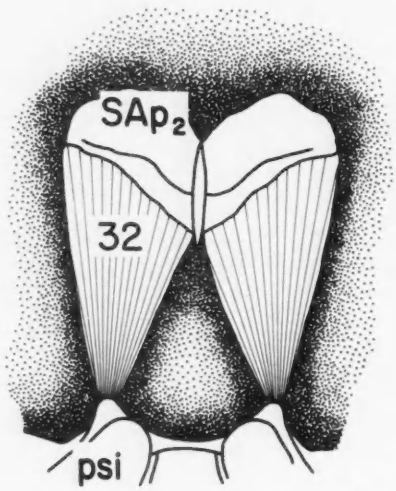

FIG. 11

PLATE 3. *Xenopsylla cheopis*. FIG. 9.—Dorsal view of the mesothoracic-metathoracic ventral longitudinal muscles. FIG. 10.—Cephalic view of the pleurosternal muscle of the metathorax. FIG. 11.—Dorsal view of the prothoracic-mesothoracic ventral longitudinal muscles.

c *Metathorax*. A pair of muscles (No. 33, fig. 9), which arises upon the laterocephalic projections of the metathoracic furca (SAp_3), extends headward to broad attachments on the caudomesal surfaces of the lateral expansions of the mesothoracic furca (SAp_2). These two bundles are so close to the meson that it is doubtful whether their alternate contraction would cause much lateral deflection of the preceding segments. Hence, their principal function appears to be that of increasing the strength of the connection between meso- and metathorax.

d. *Thoracico-abdominal Muscles*. The final pair of muscles in this series (No. 34, fig. 6) extends between the metathoracic furca (SAp_3) and the ventrolateral angles of the second abdominal sternite (II S). While the thoracic attachments approximate the meson and cover the posterior faces of the poorly developed lateral extensions of the metathoracic furca, the muscles are quite divergent posteriorly. Since the hinder margins of the metathorax overlap the basal abdominal segments, these muscles cannot be very effective in producing lateral movements, and must operate mainly to assure a firm muscular connection between thorax and abdomen.

External Coxal Muscles and Trochanteral Depressors

Although these leg muscles have been described by Landois (1866), Jacobson (1940), and Snodgrass (1946), they need to be considered here in relation to the other muscles of the thorax. The major thoracic muscle is, furthermore, a depressor of the trochanter.

Coxal Muscles:

a. *Prothorax.* As shown by Jacobson (1940) and later by Snodgrass (1946), the thoracic muscles of the procoxa are three in number. The most dorsal of this trio, a coxal abductor (No. 35, fig. 14), originates upon a marginal thickening of the inflected posterior portion of the pleurosternum (psi) and extends cephalad to an insertion upon a dorsal attenuation of the coxa (cx_1). The muscle pivots the coxa at its sclerous attachment with the prosternum.

The second conspicuous procoxal muscle (No. 36, fig. 14) is an adductor which originates upon the lateral portion of the pleurosternal inflection (psi), ventral to the abductor muscle (No. 35), and runs cephalad to its insertion upon the inner proximal rim of the coxa (cx_1).

The remaining procoxal muscle (No. 37, fig. 14) arises on the pleurosternum near the attachment of the coxa, and extends cephalomesad to its insertion upon the inner proximal rim of the coxa. It may best be categorized as a rotator of the coxa, and thus of the whole leg. Its contraction causes the cephalic aspect of the coxa, already oblique by reason of the attachment to the pleurosternum, to become even more so. The muscle (No. 37) is thus functionally the lateral antagonist of the adductor muscle (No. 36). In addition, the distal portion of the coxa contains a procoxal depressor of the trochanter as well as a coxal levator of the trochanter.

b. *Mesothorax.* The mesothoracic legs have a much diminished latitude of movement in comparison to the prothoracic legs. Primarily they abet the metathoracic legs in jumping, and their capacity for rotation has been subordinated. The sternal articular sclerite of the mesocoxa (fig. 5, q), however, does allow the leg a degree of freedom which it would not have otherwise.

Four muscles are attached to the dorsal rim of the mesocoxa and are thus involved with the movement of the coxal segment. These muscles do not participate actively in the jumping process itself, but rather control the movements of the coxa on its articulations with sternum and pleuron. As Snodgrass (1946) points out, one of these muscles arises on the pleuron while the remaining ones are of sternal origin.

The pleurocoxal muscle (No. 38, fig. 7) may be called a remotor, although this is probably its least function. As already noted under the epipleural muscles above, this muscle is stretched between the posterior rim of the mesocoxa (cx_2) and the second link plate (lp_2). Contraction of this muscle, independent of the remaining external coxal muscles, not only gives rigidity to the coxothoracic joint but also exerts a strong downward force on the cephalic end of the second link plate (lp_2). This pressure causes the caudal, upturned end of the link plate to become engaged firmly with a condyle on the second phragma (2Ph). The union between meso- and metathorax is thus strengthened greatly, and cooperation of the appendages of the two segments for violent jumping is made possible.

Similarities between the other mesocoxal muscles and the corresponding muscles of the metacoxa are so great that, although numbers have been assigned to both groups, only those of the metacoxa have been figured.

The first of the remaining mesocoxal muscles, all of which originate on the sternum, may be called a rotator (No. 39, not figured; cf. No. 44). The origin covers the entire inner face of the upturned sternum, but the muscle attenuates rapidly to its point of insertion slightly cephalad of the pleurocoxal articulation. The nature of the articulation leaves little room for coxal rotation, and the angle of muscle No. 39 with the coxa is such that the muscle might serve also as a pronator. Certainly its most important function is to strengthen the pleurocoxal joint during the jump.

The second muscle of this group (No. 40, not figured; cf. No. 45) conceivably serves as a lateral extensor. It originates on the lateral aspect of the mesosternal apodeme and extends ventrolaterad to an insertion just posterior to the pleurocoxal articulation. Its most likely action is to supplement the remotor muscle (No. 38) in strengthening the coxal articulation to the thorax.

The last of the mesothoracic sternocoxal muscles (No. 41, not figured; cf. No. 46) may be designated as coxal abductor, since its contraction causes the coxa to be withdrawn laterally. The sternal articular sclerite of the mesocoxa (fig. 5, q) is so situated as to provide a fulcrum for this action. The muscle originates upon the ventrolateral margin of the sternal apodeme and progresses ventrad to its insertion within the leg on the proximal end of the mesal ridge of the coxa. A coxal levator of the trochanter is also present.

c. *Metathorax.* As in the mesothorax, the metathoracic coxae possess four muscles, though only one of them is conspicuous. It arises on the pleural region, the remaining three on the sternum. With the exception of the pleural muscle, these metacoxal muscles are of little importance, and seem dwarfed in favor of the large and powerful trochanteral depressor.

The pleural muscle (No. 43, fig. 8) is attached over a large area of the metepimeron (epm_3) and is inserted upon the posterior margin of the coxal rim, considerably caudad of the pleurocoxal articulation. Contraction of this muscle serves to alter the relationship of the coxa to the long axis of the body. It may be termed a remotor. Although Snodgrass (1946) figures a small intraepimeral muscle in

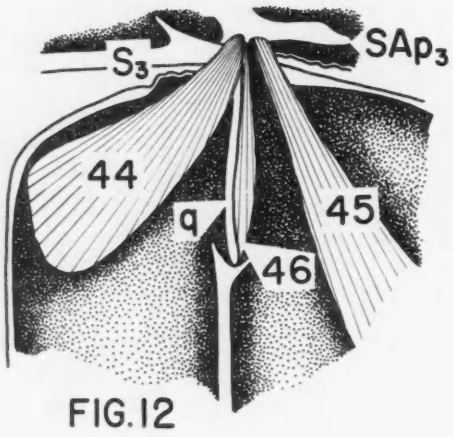

FIG. 12

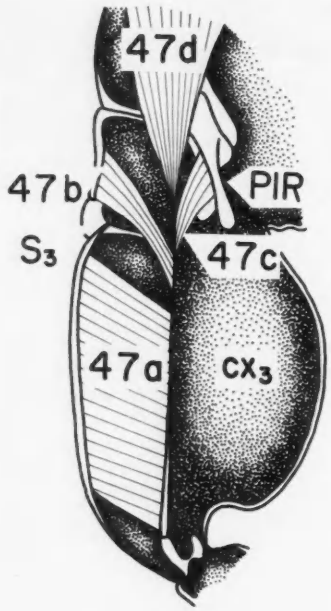

FIG. 13

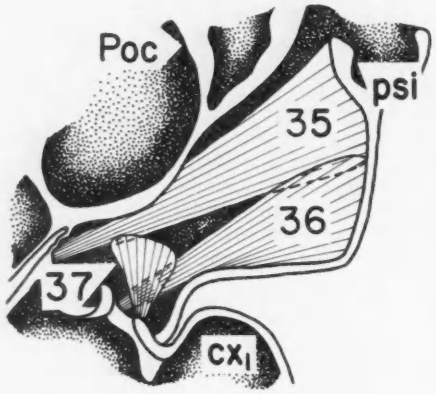

FIG. 14

PLATE 4. *Xenopsylla cheopis*. FIG. 12.—Lateral view of the remotors and promotor of the metathoracic coxa. FIG. 13.—Lateral view of the four branches of the trochanteral depressor muscle of the metathoracic leg. FIG. 14.—Lateral view of the three muscles of the prothoracic coxa.

ABBREVIATIONS AND LETTERING OF FIGURES

cr	coxal rod	Pl	pleuron
cx	dorsal lip of the coxa	PlR	pleural rod
cx_1	prothoracic coxa	Poc	postocciput
cx_2	mesothoracic coxa	psi	pleurosternal inflection
cx_3	metathoracic coxa	q	sternal articular sclerite of the coxa
epm	epimeron	S	abdominal sternite
lp_2	mesothoracic link plate	S_2	mesothoracic sternum
N_1	pronotum	S_3	metathoracic sternum
N_2	mesonotum	SAP_2	mesosternal apodeme
N_3	metanotum	SAP_3	metasternal apodeme
nf	notal flange	T	tergum
Ph	phragma	TB	tentorial bridge

Dactylopsylla bluei (C. Fox), which he calls an intra-epimeral muscle, no such muscle was found in *X. cheopis*.

A small metacoxal promotor (No. 44, fig. 12) originates on the sternum cephalad of the sternocoxal articulation and is inserted within the anterior coxal rim.

A second remotor muscle (No. 45, fig. 12) arises on the sternum caudad of the sternocoxal articulation, and is inserted within the posterior coxal rim.

The last and least conspicuous of the metacoxal muscles may be called a flexor (No. 46, fig. 12). It is attached directly to the condyle of the sternocoxal articulation and is inserted upon the distal end of the mesal articular sclerite (q) of the coxa.

Collectively, these metacoxal muscles serve to increase the integrity of the sternocoxal joint. Their simultaneous contraction, no doubt, lends an appreciable degree of rigidity to the connection.

Trochanteral Depressors:

a. *Prothorax*. Thoracic branches of the trochanteral depressor are lacking in this segment in *X. cheopis*, although Snodgrass (1946) notes them in some other forms.

b. *Mesothorax*. The depressor of the trochanter of the middle leg (No. 42, not figured; cf. No. 47) has four branches, all inserted on a short tendon which arises on the proximal rim of the trochanter and extends dorsad through the coxa. The first branch (No. 42a) originates on the anterior inner surface of the coxa. The second branch (No. 42b) attains its identity while still in the coxa, but passes into the mesothoracic cavity to its origin on the rim of the cephalic inflection of the sternum. Snodgrass (1946) refers to this branch as being episternal in insertion. The third branch (No. 42c), apparent only in transverse sections of the flea, simply diverges slightly from the main body of the muscle to an origin on the pleural rod. The fourth and largest branch (No. 42d) is the major muscle of the mesothorax. Its origin occupies the greater part of the notal surface but does not cover the mesal region, which is filled by the longitudinal dorsal muscles (No. 25). Insofar as the mesothorax is involved in the jumping of the flea, it is the trochanteral depressor muscle (No. 42) which is directly concerned.

c. *Metathorax*. The trochanteral depressors of the metathoracic legs (Nos. 47, fig. 13) are without doubt the most important locomotor muscles in the body of the flea. Aided by the similar muscles of the mesothoracic legs (No. 42), their sudden contraction gives the Siphonaptera powers of leaping far greater, relatively, than are displayed by members of any other order. Originally it was this capacity of the fleas that attracted more attention from investigators than all the other fascinating aspects of their anatomy and biology combined.

Muscle No. 47 compares favorably with its mesothoracic homolog (No. 42) in its four-branched structure and the disposition of its parts. All the branches are inserted on the common depressor tendon which arises from the trochanter. The first branch (No. 47a) does not enter the thorax at all, but originates on the cephalic wall of the coxa. Branch 2 (No. 47b) extends ventrocaudad from its origin on the cephalic inflection of the metasternum to its insertion within the coxa on the depressor tendon. The third branch (No. 47c) is attached to the pleural arm slightly ventrad of the latter's fusion with the notal arm, and is inserted on the depressor tendon a little above the insertion of No. 47b. The origin of the enormous fourth branch (No. 47d) extends over most of the internal surface of the metanotum.

The mechanism of the jump, and the musculature of the remaining leg segments, have been discussed in detail by previous workers. The earliest mention of them was made by Landois (1866). More accurate and thorough accounts of the structure and function of the thoracic appendages are given by Jacobson (1940) and by Snodgrass (1946).

DISCUSSION

As is seen from the preceding description, the number of thoracic muscles in *X. cheopis* is drastically reduced in comparison with that normally found in less specialized insect groups. Table 1 has been constructed as a convenient summary of this situation. A strong correlation is evident, also, between the loss of many of these muscles and the absence of wings. Concurrently, the muscles most directly concerned with jumping have become greatly increased in size.

Table 1.—Reduction of typical muscle classes in the flea.

Muscle classes found in Pterygota	Distribution of thoracic muscles in the flea		
	Pro-thorax	Meso-thorax	Meta-thorax
Dorsal	+	+	+
Tergopleural	—	—	—
Tergosternal	—	—	—
Axillary	—	—	—
Epipleural	—	+	+
Lateral intersegmental	+		—
Pleurosternal	—	+	+
Ventral	+	+	+

Speaking generally, the surviving muscles in the flea fall into two groups in reference to their function: those which are immediately involved in movement, and those whose task it is to increase the integrity of the body. The high degree of specialization of the siphonapteran musculature for the second of these functions has resulted in a thoroughly integrated thoracic unit within which the locomotor muscles may perform with maximum efficiency, and which is an essential element in the exceptional jumping prowess shown by the flea.

Although the thoracic segments are thus specially adapted to cope with the violent stresses of this un-

usual activity, they are, at the same time, allowed a high degree of lateral flexibility. Too much emphasis seems to have been placed hitherto upon the exceptional jumping powers of the flea, and too little emphasis upon the anatomical requirements of an ectoparasitic existence. There is little doubt that saltation is of the utmost advantage to fleas in gaining access to new hosts, especially in forms that are not limited to doing so in the host nest. Once access has been gained, however, conditions on the body of the host impose an entirely new set of requirements. Of utmost importance is the ability of the ectoparasite to maneuver successfully through the pelage without losing its purchase upon the host. Since, in most cases, the fur is of such length and density that the flea must make its way through rather than over the coat, lateral flexibility is of unquestionable advantage. That these diametrically opposed requirements have been satisfied most economically by the skeletal and muscular modifications of fleas is attested by the high degree of structural homogeneity of the Siphonaptera, which is unparalleled in other insect orders.

One of the primary objectives of this inquiry was to determine whether the thoracic musculature of the flea might supply some clue as to the ancestry of the order. As has been indicated, however, *X. cheopis* is highly specialized anatomically, and is so thoroughly adapted to its ectoparasitic existence that its structure throws little light on its relationships with other insects. The internal as well as the external systems have been affected. It may be said that the study of the musculature of *Xenopsylla* has provided little comfort for those who would derive the Siphonaptera from either the Coleoptera or the Diptera. Existing representatives of both these orders are themselves muscularly specialized in ways which seem to preclude the derivation of the Siphonaptera directly from them.

Snodgrass (1946) summarizes the evidence on the origin of the fleas in the first paragraph of his work upon the exoskeleton. The presence of papilliform rectal organs and the two-segmented parameral claspers which are separate from the aedeagus seems to indicate common origin with the Mecoptera, Trichoptera, Lepidoptera, and Diptera. As was mentioned above, no special affinity with the Diptera is attested by the musculature. The presence in the prothorax of *Xenopsylla* of the transverse interfurcal muscle (No. 31), which is a characteristic pecularity of mecopteran species, would seem to bolster the notion of a closer relationship between the scorpion flies and the fleas; but the fact that a similar arrangement of this muscle occurs in the distantly related Mallophaga (Mayer 1954) cautions one against relying on this datum as evidence that the Mecoptera and Siphonaptera are of close common descent.

In speculating upon the origin of the fleas it does seem reasonable, however, to postulate the presence, during the Middle Cretaceous period, of a holometabolous insect which associated with the few mammals then extant. Since it was during the Late Cretaceous period that mammals gained their ascendancy, it may further be postulated that during this time the Siphonaptera began to evolve. Fossil records indicate that the most common holometabolous insect order at this time was the Mecoptera. Conceivably, some family or other representative section of this order was the group which found new pasture upon the rapidly increasing mammalian population.

Representatives of the Mecoptera possess several characteristics in addition to those already mentioned that lend support to such speculation. First they are generally conceded to be primarily predacious. Even though their predation is mostly limited to other insects, the tendency toward a high protein diet is nonetheless manifest. Once such a tendency becomes established, new pathways of evolution are automatically opened. Further, as Potter (1938) points out, the Mecoptera and Siphonaptera share the possession of sexually dimorphic central nervous systems; that is to say, the males of both orders have eight abdominal ganglia while the females have but seven. These two characteristics, in conjunction with the fact that secondary winglessness is recurrent in the order Mecoptera, makes some early mecopteran type a likely nominee for the ancestor of the fleas, as Tillyard (1935) has proposed.

Although the evidence summarized does by no means prove that the Siphonaptera are of mecopteran origin, it does make clear that the features which the two groups hold in common are of sufficient magnitude and number to deserve full attention in any phylogenetic consideration of the order Siphonaptera.

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The Reproductive System of Some Florida Mosquitoes. I. The Male Reproductive Tract[1]

PATRICK T. M. LUM

Entomological Research Center, Vero Beach, Florida

ABSTRACT

A comparative system of the anatomical arrangement was made on 10 species, namely, *Aedes triseriatus, A. taeniorhynchus, A. fulvus pallens, A. infirmatus, Psorophora howardii, Culex pipiens quinquefasciatus, Deinocerites cancer, Uranotaenia lowii, Culiseta inornata,* and *Anopheles crucians.* The chief differences found were in the shape of the accessory glands, the time of formation of mature spermatozoa, and particularly in the arrangement of the seminal vesicles. The accessory glands were oval, or elongate, or pear-shaped; in *U. lowii* and *A. taeniorhynchus* they were shaped differently in newly emerged males than in older ones. In the *Psorophora,* the *Culex,* and the four *Aedes* species the seminal vesicles were conjoined or fused throughout their length, but in *C. inornata, D. cancer, U. lowii,* and *A. crucians* they were separate, connected only at the posterior ends. In the species with conjoined or fused vesicles the transfer of spermatozoa was rapid (10 to 15 seconds) during mating, but this was prolonged to 45 minutes or more in three of the four species with separate vesicles; mating behavior was not observed in *Anopheles crucians,* which is strikingly different from all the other nine species in the size and musculature of its ejaculatory duct. Active spermatozoa were found in the seminal vesicles within 15 minutes after emergence in *P. howardii, D. cancer,* and *U. lowii*; after 6 hours in *A. taeniorhynchus, A. triseriatus, A. infirmatus, C. p. quinquefasciatus, C. inornata,* and *A. crucians*; and after 20 hours in *A. fulvus pallens.*

Although extensive anatomical and physiological information is available for various female mosquitoes (Wigglesworth 1949, Snodgrass 1959, Christopher 1960), strikingly little data exists for the male. Most of the morphological information on the male is concerned with the anatomy of the reproductive apparatus (Prashad 1916, Perfil'ev 1930, Edwards 1941, Hayes 1953, Burcham 1957, Hodapp 1960, Christopher 1960). The comparative study by Prashad (1916) of the internal anatomy of the reproductive system of five species and four genera of mosquitoes indicated no less than three distinct anatomical arrangements. Perfil'ev (1930) did an excellent study of *Anopheles* mosquitoes, but found the arrangements of the organs and ducts were essentially uniform in this genus. Both these papers, by Prashad and by Perfil'ev, were morphological and their authors did not relate their observations to the mating behavior of the species.

In the present study 10 species of mosquitoes—*Aedes triseriatus* (Say), *Aedes taeniorhynchus* (Wiedemann), *Aedes fulvus pallens* Ross, *Aedes infirmatus* Dyar and Knab, *Psorophora howardii* Coquillett, *Culex pipiens quinquefasciatus* Say, *Deinocerites cancer* Theobald, *Uranotaenia lowii* Theobald, *Culiseta inornata* (Williston), and *Anopheles crucians* Wiedemann— were used to show: (1) the arrangements of the reproductive tracts of the different species, (2) the condition of the testes, vasa deferentia, seminal vesicles and accessory glands in the male at various intervals after emergence, and (3) the general relationship of the anatomical arrangements of the reproductive tract to the length of time in copula of the male.

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METHODS

The reproductive tract was dissected in a modified insect "Ringer" solution (7.5 gm NaCl, 0.135 gm KCl, 0.135 gm $CaCl_2$ and 0.120 gm $NaHCO_3$ in 1 liter of H_2O) in the following manner: (1) the abdomen was severed from the thorax, (2) the sternite and tergite of each abdominal segment were gently pulled apart at the membranous pleura until the whole abdomen was opened, and (3) all tracheal and nerve connections were cut prior to removing the entire tract. To avoid stretching of the ducts and glands, a dissecting needle was used to lift the isolated tract out of the abdomen. The preparations were studied with and without the use of cover-slips, under magnifications ranging from 200X to 450X.

Observations on mating behavior were made on colonies which were already established in the laboratory. *Psorophora howardii, A. taeniorhynchus, A. triseriatus, C. p. quinquefasciatus, D. cancer, U. lowii,* and *C. inornata* mated readily in cages under laboratory conditions of controlled lighting. The species which did not mate under caged conditions, *A. fulvus pallens* and *A. infirmatus,* were artificially induced to mate using the technique of McDaniel and Horsfall (1957). No observations were made on the mating behavior of *Anopheles crucians.* All species

of the mosquitoes examined were maintained at 25° to 27° C. and at 50% to 70% relative humidity, and both males and females were fed a 10% sucrose solution.

RESULTS

The reproductive tract of male mosquitoes (fig. 1) consist of the testes, vasa deferentia, seminal vesicles, accessory glands, and ejaculatory duct. The arrangement, size, and shape of the various structures in different genera were found to vary considerably.

Testes.—Except in *A. fulvus pallens*, the testes were uniformly elongated and possessed spermacysts. The posterior portions of the testes contained apparently mature spermatozoa, whereas the anterior parts had spermacysts with immature spermatozoa. In *A. fulvus pallens* the testes were oval in shape.

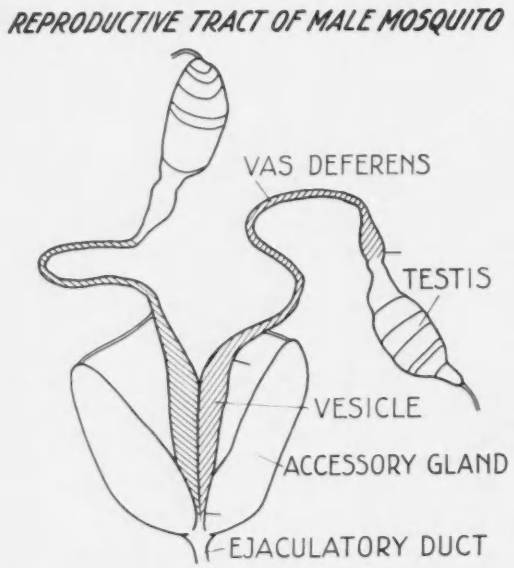

FIG. 1.—Diagrammatic sketch of the male reproductive tract of *Aedes Infirmatus*, showing the basic glands and ducts and the conjoined seminal vesicles.

In all species a coat of fat, colorless or with either a dark brownish (*Aedes, Psorophora, Culex, Deinocerites, Uranotaenia,* and *Anopheles* spp.) or reddish pigmentation (*Culiseta*), surrounded each testis and obscured its true shape.

Undulating or active spermatozoa in the posterior portions of the testes were seen only in newly emerged males of *P. howardii, D. cancer,* and *U. lowii,* although no spermatozoa had begun their movement to the seminal vesicles. In the testes of *A. taeniorhynchus, A. infirmatus, C. p. quinquefasciatus, A. crucians* and *C. inornata,* spermatozoa did not begin to undulate until 5 hours after emergence or 20 hours in the case of *A. fulvus pallens.* In all cases the undulation of spermatozoa in the posteriormost spermacysts of the testes was the prelude to the movement to the seminal vesicles.

The formation of mature spermatozoa in the testes, once begun, continues until the spermacysts are exhausted of spermatogonia. In males examined after 25 days the testes have shrunk considerably with usually two or three spermacysts remaining. In males which are kept from mating the numerous spermatozoa, after filling the vesicles and vas deferens, are stored in the posteriormost portion of the testes. In mated males, however, the spermatozoa are continuously leaving the testes to enter the vesicles, consequently few mature spermatozoa are found stored in the testes. Contrary to this observation are those made by Professor Jack Colvard Jones, University of Maryland (personal communication) in which the testes as well as the seminal vesicles of *Aedes aegypti* (Linnaeus) were seen to store mature spermatozoa in both mated and unmated males.

Vas deferens.—Long, thin ducts running from the testes to the seminal vesicles are found in the males of all 10 species. In *C. inornata* the ducts are much shorter than in those of the other species. The vasa deferentia which open into the seminal vesicles are devoid of spermatozoa in the newly emerged males of all species. Instead, the lumens of the ducts are filled with a colorless fluid containing very fine granules. This fluid moves up and down with the contractions of the seminal vesicles and vas deferens, thus presenting a medium for the spermatozoa to travel in as they leave the testes to enter the seminal vesicles. The granules in the fluid gradually disappear as the spermatozoa enter and fill the lumen. Like the testes, the vasa deferentia serve as additional storage sites for mature spermatozoa when the seminal vesicles are filled. Dissection of the ducts from males which were prevented from mating revealed that the spermatozoa were as active as those which were stored in the seminal vesicles. Both undulatory and locomotory motions were displayed by these spermatozoa.

Seminal vesicles.—The seminal vesicles in the various species were either joined together throughout their length, or separated for most of their length but joining just before the entrance of the accessory glands into the ejaculatory duct. Fused or joined seminal vesicles were found in all of the *Aedes* (fig. 2), *P. howardii,* and *C. p. quinquefasciatus.* Fused vesicles are, however, sometimes capable of separating, e. g., in *A. taeniorhynchus* they were found separated after repeated forced copulation, but this is rare. Separated seminal vesicles were encountered in *D. cancer, U. lowii, A. crucians* (fig. 6) and *C. inornata.* In these species the distention of the vesicles clearly marks the region of the vas deferens where spermatozoa collect. Joined or fused vesicles were seen to contract in unison but separated vesicles contracted independently of each other.

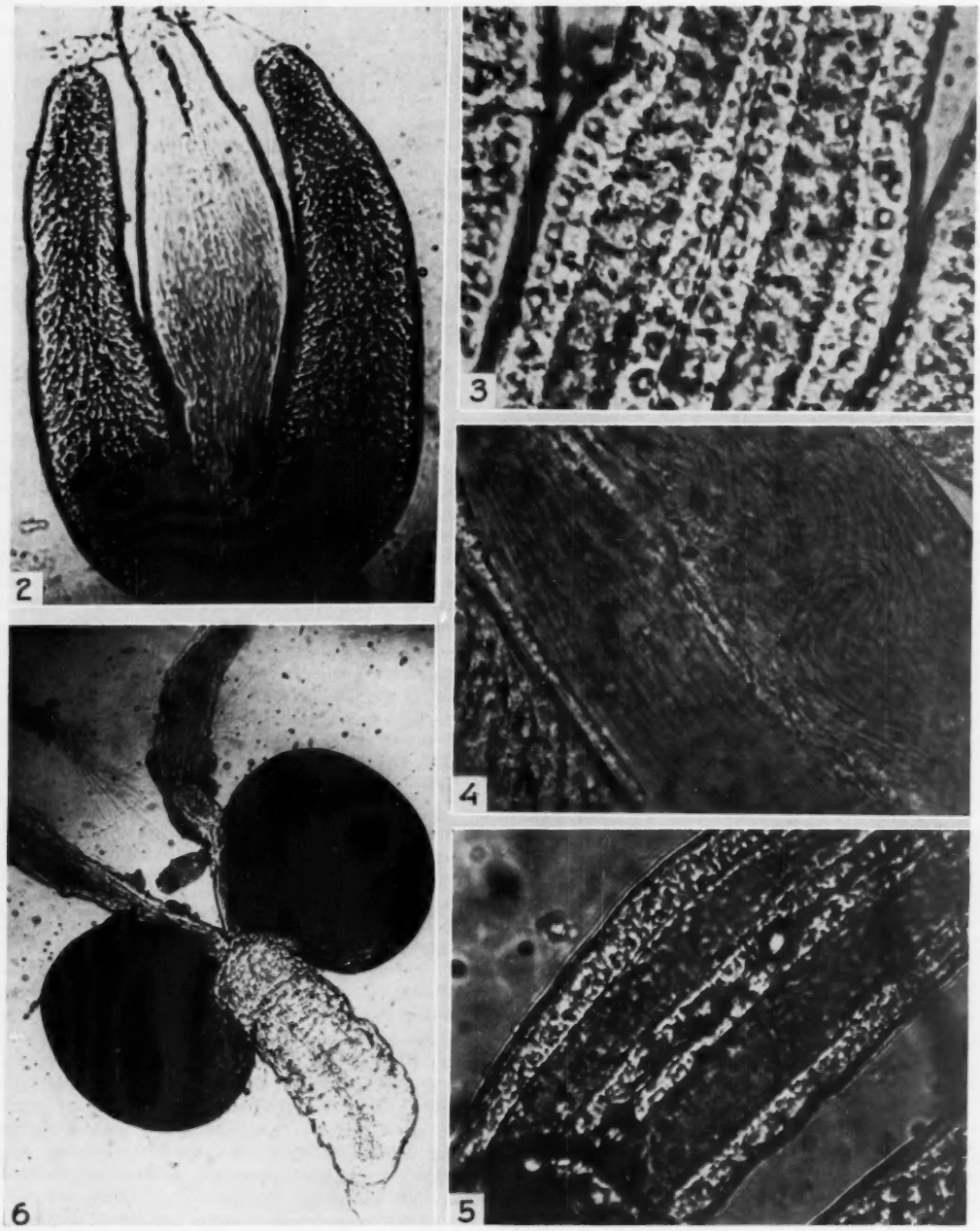

FIG. 2.—Elongated accessory glands and connected seminal vesicles of 48-hour-old male *Aedes taeniorhynchus*. FIG. 3.—Portion of the seminal vesicles of a newly emerged male of A. taeniorhynchus. No spermatozoa are present. FIG. 4.—Portion of the seminal vesicles of a 48-hour-old male of *A. taeniorhynchus*. FIG. 5.—Portion of the seminal vesicles of a 48-hour-old male of *A. taeniorhynchus* after mating. The row of cells in the wall is no longer distinguishable. FIG. 6.—Oval accessory glands, separated vesicles, and muscular ejaculatory duct of *Anopheles crucians*.

Prashad (1916) showed the paired vasa deferentia of *C. p. quinquefasciatus* uniting to form a "single vesicle" which then formed the "sacculus ejaculatorius" from which the ductus ejaculatorius arose. He also stated that the "sacculus ejaculatorius" is demarcated by a constriction from the seminal vesicle and that both regions serve as storage for mature spermatozoa. In this present study no "sacculus ejaculatorius" was found in any of the species examined; the seminal vesicles, vasa deferentia, and testes were the only sites where spermatozoa were stored. The constriction between the "sacculus ejaculatorius" and seminal vesicles which Prashad (1916) noted was often seen in males which mated. When filled with spermatozoa the distended walls of the seminal vesicles are entirely smooth. Immediately after mating the walls of the vesicles show irregular constrictions or folds which vary in number and location. These constrictions or folds may account for the observations by Prashad.

As seen in fig. 3 the lumens of the vesicles in the newly emerged male are narrow. The thick walls of the vesicles are composed of a row of cells. As the spermatozoa enter the seminal vesicles, the lumens gradually enlarge and in 48 hours the seminal vesicles become greatly distended and the once-thick walls transform to thin membranes (fig. 4). Conceivably the cells lining the walls of the vesicles are secretory in nature. After mating, in which the vesicles have lost part of their contents, the row of cells is no longer distinguishable in the walls (fig. 5).

Once spermatozoa become active in the testes it is only a matter of 15 to 30 minutes before they are found in the seminal vesicles. Spermatozoa were found in the vesicles shortly after 15 minutes beyond emergence in the males of *P. howardii, U. lowii* and *D. cancer,* 6 hours after emergence in *A. taeniorhynchus, A. crucians, C. p. quinquefasciatus, A. infirmatus, C. inornata, A. triseriatus,* and 20 hours after emergence in *A. fulvus pallens.* In all of the males examined spermatozoa were present in great numbers in the seminal vesicles 48 hours after emergence.

Accessory glands.—Among the 10 species of mosquitoes examined in this study, the shape of the accessory glands varied not only among the different genera but also within a single genus. In *U. lowii, P. howardii, C. p. quinquefasciatus,* and *A. taeniorhynchus* the glands were pear-shaped; in *A. crucians* they were oval; in *C. inornata* the glands were elongated; in *D. cancer* they were also elongated but constricted slightly in the center. The accessory glands in *A. infirmatus* were also elongated and similar to those of *A. fulvus pallens.* The glands of *A. triseriatus,* although elongated like those of the *Aedes* described, were distinctly different in that a constriction at the center of each gland divided it into seemingly separate but connected portions. The lower portion of the gland was denser in appearance and more opaque, containing a fluid which was not as granular as that found in the upper portion of the gland.

In the case of *U. lowii* and *A. taeniorhynchus* the glands change shape after emergence. In a newly emerged male of *U. lowii* the glands are oval and as the male becomes older the glands then become pear-shaped. Under transmitted light the material within the accessory gland can also be seen to increase in amount as they change in shape. In *A. taeniorhynchus* a similar change occurs. In the newly emerged male they are ovate with the anterior tips blunt and round, but in 24 hours the glands become elongated. Because of these changes, definite examinations were made on males 48 hours or more older.

The filaments connecting the anterior tips of the accessory glands to the vasa deferentia were found in eight species but were absent in *A. crucians* and *U. lowii.*

The accessory glands normally do not store active or mature spermatozoa, however, during routine examinations of the accessory glands in males of *A. taeniorhynchus* and *P. howardii* a few spermatozoa were occasionally seen in the accessory glands. Perhaps pressure from the coverslip accounts for this finding.

Ejaculatory duct.—As described by Snodgrass (1935), the ectodermally derived ductus ejaculatorius in insects possesses a strong muscular sheath which surrounds the epithelial wall of the duct. In all the species except *A. crucians* the ejaculatory duct was very similar in shape and size and inconspicuous in musculature, whereas the duct in *A. crucians* was not only larger in size but heavier in musculature (fig. 6). Under magnifications of 400X the contractions of the duct could be easily seen in this species, whereas those of the other species were hardly discernible.

Mating Behavior.—Copulation, natural or artificially manipulated, was observed for all species studied except *A. crucians.* The transmission of spermatozoa was rapid, requiring only a few seconds in all of the *Aedes,* in *P. howardii,* and in *C. p. quinquefasciatus.* In these mosquitoes the seminal vesicles are fused. *Deinocerites cancer, U. lowii,* and *C. inornata* possess separated seminal vesicles and differed from mosquitoes having joined seminal vesicles in the length of time required for the transfer of spermatozoa. Copulation in *D. cancer* (Haeger and Phinizee 1959) and *U. lowii* required approximately 45 minutes or more and in *C. inornata* mating pairs were observed to remain in copula for over 50 minutes. Rees and Onishi (1951) reported 6 hours and 40 minutes for *C. inornata.* It is suggested that the separated seminal vesicles contract independently of each other and thus do not ejaculate as rapidly as those with joined vesicles. If such is the case, and the time required for mating in mosquitoes is reflected in the anatomical arrangements of the seminal vesicles, workers in the field who are interested in the colonization and mating behavior of mosquitoes may find it worthwhile to make a preliminary examination of the anatomy of the species concerned.

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The Genera of Platystomatidae and Otitidae Known to Occur in America North of Mexico (Diptera, Acalyptratae)[1]

GEORGE C. STEYSKAL

27253 West River Road, Grosse Ile, Michigan

ABSTRACT

The Otitidae in the broader sense (=Ortalidae of Loew, less the Pyrgotidae which have generally been considered for some time to be a distinct family) are treated as three families, Richardiidae, Platystomatidae, and Otitidae, the latter including the Otitinae and Ulidiinae, while the "Pterocallidae" are considered to be of less than subfamily rank within the Otitinae. Reasons based upon the structure of the male postabdomen are adduced for this classification and keys to the genera of the Platystomatidae and Otitidae are provided, the Richardiidae having been treated previously. The following new genera and species are proposed, all in Otitidae: **MYIOMYRMICA** (Otitinae; type *Cephalia fenestrata* Coq.); **TUJUNGA** (Otitinae; type *T.* **mackenziei,** California); **HAIGIA** (Otitinae; type *H.* **nevadana,** Nevada); **ULIDIOTITES** (Otitinae; type *U.* **dakotana,** South Dakota, Nebraska); and **TEXASA** (Ulidiinae; type *T.* **chaetifrona,** Texas). New synonymy: *Tetropismenus* Loew (=*Califortalis* Curran), their type species *T. hirtus* Loew (=*C. hirsutifrons* Curran) being synonymous; and *Otites* Latreille (=*Ortalimyia* Curran). *Psaeropterella* Hendel and *Eurycephalomyia* Hendel are reduced to subgenera under *Tetanops* Fallén.

The only keys to the genera of North American Otitidae (in the broader sense) that have appeared since the Loew Monograph (1873) are those of Hendel (1909-14) and Curran (1934), both of which are now seriously out of date; and Hendel never did treat the Otitidae in the narrower sense. Hennig (1939-45) made the first major revision in the classification of the higher categories in his great monograph of the Palaearctic fauna. I am here endeavoring to extend Hennig's lead to the North American fauna.

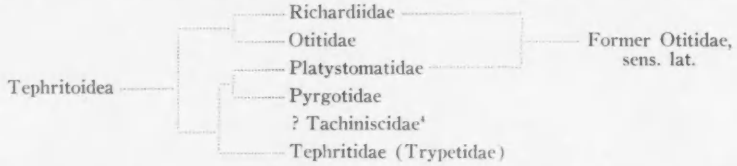
Hennig used characters of the male postabdomen, chiefly those of the aedeagus: whether the shaft is provided with hairs or bristles or whether it is bare, and the nature of the tip or glans. My studies have confirmed Hennig's conclusions, and in making comparisons of the parts of the postabdomen I have come upon other characters which appear to be of significant value.

The characters used by Loew and Hendel, such as those of the setae on wing vein r_1, the nature of the anal cell, and the propleural bristle, have been found (Hennig 1958: 573-83) to be so complicated by convergent development and secondary loss as to be extremely difficult to use and to evaluate properly. Consequently, several of the genera assigned by Loew and Hendel to certain subfamilies (families) have been found to belong elsewhere. The Cephalina of Loew (Myrmecomyiina of Hendel), for example, was considered by Loew to be a distinct group of coordinate rank with the Pyrgotina, Platystomina, Ortalina, Pterocallina, Ulidina, and Richardina, while

[1] Accepted for publication September 26, 1960.

Hendel considered it to be a subordinate group within the Platystominae; its members have now been found to be somewhat specialized Otitidae (Ortalina).[2]

Since Hendel (1916, 1922) divided the Acalyptera-tae into superfamilies, designating the one to which the present group belongs as the Tephritoidea,[3] a change of type initiated by Frey (1921) in erecting the Ortalidiformia has resulted in the superfamily becoming known as the Otitoidea. This superfamily, after several changes in content by various authors, now comprises (Hennig 1958) the families that I would arrange in a phylogenetic chart as follows:



Loew recognized but two families here, the Trypetidae and the Ortalidae. The Trypetidae remain essentially as he defined them; his Ortalidae included the remainder of the families now recognized. Curran (1934) recognized three families, Tephritidae (as Trupaneidae), Otitidae, and Pyrgotidae. Others, such as Brues, Melander, and Carpenter (1954), have recognized additional groups as families: Ulidiidae, Pterocallidae, and Phytalmiidae, the latter a group of the New Guinean region which Hennig has shown to be partly Tephritidae and partly Platystomatidae. Some discussion of family relationships will be found below in general discussion of each group.

KEY TO THE FAMILIES OF TEPHRITOIDEA FOUND IN NORTH AMERICA

1(2). Inferior orbital bristles present; costa interrupted some distance apicad of humeral crossvein, the subcostal vein weakening to a fold that extends rectangularly to the costal interruption; propleural bristle rarely present; aedeagal apodemes fultelliform[5] ..... TEPHRITIDAE

2(1). Inferior orbital bristles lacking, although large hairs on lower front may be present; costa unbroken, or, if broken, subcosta practically complete; propleural bristle often well developed.

3(4). Ocelli lacking; ovipositor stout basally, large and long; aedeagal apodeme fultelliform ..... PYRGOTIDAE

4(3). Ocelli present; ovipositor much smaller.

5(6). Costa interrupted at tip of *sc*, which ends some distance from tip of r_1, but not interrupted close beyond humeral crossvein; anal cell never with pointed lower corner or extension, vein closing anal cell straight or recurved; sternopleural bristle seldom lacking; basal abdominal tergites usually with erect bristles laterally; at least hind femora usually with spines below; aedeagus lacking apodeme, bare, with tip simple or specialized, but never with glans of platystomatid type (exclusively American, largely tropical) ..... RICHARDIIDAE

6(5). Costa uninterrupted, or interrupted close beyond humeral crossvein and not at tip of r_1; anal cell often with pointed or extended lower corner; basal abdominal tergites without erect bristles laterally; femora usually without spines below; aedeagus various, but always with apodeme.

7(8). Anal cell lengthened, on upper side more than 0.25 of length of lower side of discal cell, never with point in lower corner; sternopleural bristle lacking in American genera; wing vein r_1 setulose; propleural bristle weak or lacking; aedeagal apodeme fultelliform, aedeagus bare and with characteristic, spindle-shaped glans (cf. figs. 1-3) ..... PLATYSTOMATIDAE

8(7). Anal cell short, on upper side usually less than 0.25 of length of lower side of discal cell (lacking in *Steneretma*), if longer usually with pointed or extended lower corner (absent only in *Homalocephala, Hiatus, Haigia, Curranops, Tujunga, Delphinia,* and some species of *Tritoxa*); sternopleural bristle present (except in *Myrmecothea*); r_1 bare or setulose; propleural bristle sometimes well developed; aedeagus with cuneiform or Y-shaped apodeme, bare or furnished with teeth, bristles, or hairs on shaft, and tip simple or complex but not of the platystomatid type (cf. figs. 4-13, 15, 16) ..... OTITIDAE

FAMILY RICHARDIIDAE

A résumé of the regional species, together with some descriptions of the male postabdomen, was recently presented (Steyskal 1958). Additional examination of the male inner copulatory apparatus shows that the aedeagal apodeme is lacking or very small, a trend foreshadowed by certain Ulidiinae, and the aedeagus is supported by what apparently are extensions of the hypandrium. The pair of claspers that I have called "postgonites" may be derivatives of the 10th sternite (epiphallus); see also below under Otitidae.

FAMILY PLATYSTOMATIDAE

The presence here of an aedeagal apodeme in the form of a fultella, as described by Munro (1947), wherein a pair of lateral arms project to the hypandrial ring (figs. 1-3, f), removes this group sharply from the Otitidae and Richardiidae and aligns it with the Tephritidae and Pyrgotidae.

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[2] The generic name Ortalis is preoccupied. Although the name that replaces it is *Ceroxys*, my proposal (*in* Sabrosky 1946: 168) to call the family Ceroxydidae has met with no response, and it now seems wise to use the family name Otitidae, based upon *Otites*, as Aldrich (1932) proposed when he called attention to the preoccupation.

[3] Based upon the generic name *Tephritis*. Sabrosky (1946: 167) has recommended the retention of *Trypeta* as the basis of supergeneric group names.

[4] The Tachiniscidae are still doubtful. Although the description of *Tachinisca* (from South America) by Kertész (1903) was remarkably complete, the postabdomen remains undescribed. The African genera *Anthophasia* and *Tachiniscidea* (see Malloch 1931) differ in important respects, and their postabdomens also remain undescribed.

[5] With lateral processes extending to the hypandrial ring; cf. discussion under Platystomatidae and figures 1-3, f.

A sclerite which appears to be derived from the 10th sternite and therefore an epiphallus, as defined by Hennig (1958), seems to be present at least in *Senopterina brevipes* (fig. 1B, ep). In *Pogonortalis doclea* (fig. 2) the "outer claspers" of Munro, the epiphallus forming the posterior margin of the hypandrium, and the U-shaped anterior epandrium are all fused together.

A strongly sclerotized, bilobate cap on the ejaculatory apodeme (*ejc*), where the other groups have only a highly transparent, colorless vesicle, also seems characteristic of the Platystomatidae.

But a small fragment of the family occurs in the Americas, only three indigenous genera being known from north of Mexico, plus a representative of an Indo-Australian genus, *Pogonortalis doclea* Walker, which has been found in California. All of our genera have a long third antennal segment extending approximately to the oral margin.

KEY TO THE GENERA OF PLATYSTOMATIDAE KNOWN TO OCCUR NORTH OF MEXICO

1(2). Wing vein m_1 dipping downward into discal cell just basad of *ta*; abdomen somewhat cylindrical basally; two short *fo* ..... **Rivellia** R.-D.

2(1). Wing vein m_1 straight on both sides of *ta*.

3(4). Abdomen broad basally, rather short and flat; thorax not longer than wide; two small *fo*; cell R_5 not narrowed apically ..... **Amphicnephes** Loew

4(3). Abdomen narrower, somewhat compressed laterally.

5(6). *Ta* oblique, beyond middle of discal cell; cell R_5 parallel-margined or slightly narrowed apically; color more or less metallic blue, green, or violet; mouth-opening ordinary ..... **Senopterina** Macq.

6(5). *Ta* perpendicular, before middle of discal cell; cell R_5 distinctly narrowed apically; body reddish to dark brown, not metallic; mouth-opening, especially in male, broad and margined laterally with long hairs ..... **Pogonortalis** Hendel

A revision of our species of *Rivellia*, using characters of the aedeagus, has been presented by Namba (1956).

FAMILY OTITIDAE

European workers, especially, have considered the Ulidiinae to be of family rank, although Hennig (1939) showed that the only thorogoing distinction between the Ulidiinae and the Otitinae lies in the aedeagus:

1(2). Aedeagus bare, sometimes with specialized endstructure (figs. 10C, 11, 12); wing vein r_1 bare (except in *Homalocephala*, some species of *Euxesta* and *Acrostica*, and in the extralimital *Pareuxesta* and *Neoeuxesta*) ..... ULIDIINAE

2(1). Aedeagus bristly or hairy, more or less simple at tip (figs. 4-9, 15, 16); wing vein r_1 setulose apically (except in *Ulidiotites*, *Tujunga*, *Notogramma*, and some species of *Seioptera* and *Curranops*) ..... OTITINAE

Hennig (1939) also pointed out that the Cephalina (Myrmecomyiinae) are otitine, a fact that I have confirmed in our genera *Myrmecothea* and *Myiomyrmica*.

Many authors have also considered the Pterocallinae to be a distinct family. I would consider them to be merely specialized (apomorphic) Otitinae, since, except for the peculiar wing shape and venation, they have the characters of that subfamily.

Even the aedeagal characters break down in the case of the new genus *Ulidiotites* which, although it has a bristly aedeagus, has the ulidiine characters of bare r_1 and angularly extended anal cell. Quite surprisingly, the genus *Notogramma* has revealed an otitine postabdomen (fig. 16), wherein the aedeagus has a few triangular teeth, then some bristles, and finally numerous hairs.

Hennig (1958) stated that no trace of the epiphallus (10th sternite of the male postabdomen) could be found in the otitid groups. In the genera *Stictomyia* (figs. 11, 12), *Texasa* (fig. 10), and *Oedopa* such a structure is apparent. Some indication that the 10th sternite has entered into the formation of the structure that Munro (1947) calls "outer clasper" is afforded by *Physiphora demandata* (fig. 13), the Platystomatidae of figures 1 to 3, and the Otitinae *Idana marginata* (fig. 4) and *Haigia nevadana* (fig. 15B). The structures in the Richardiidae that I (Steyskal 1958) have called postgonites may also be derived from the 10th sternite.

A pair of rudimentary sclerotic areas at the base of the aedeagus is found in *Physiphora demandata* (fig. 13, *x*) and in *Myrmecothea myrmecoides* (fig. 6B, *x*), and four such areas are found in the African tachiniscid *Anthophasis fenestrata* (unpublished data). These may well be rudiments of pregonites and postgonites.

Much work remains to be done on the male postabdomen in the Tephritoidea, work that can be expected to throw additional light on the relationships between groups.

The genera of our fauna, on the basis of bristled or nonbristled aedeagus (except in the genera marked with an asterisk, indicating those whose postabdomens I have not examined), may be referred to subfamily as follows:

OTITINAE

Callopistromyia
Cephalia
Ceroxys
Curranops
Delphinia
Diacrita
Dyscrasis
Haigia
Herina
Hiatus
Idana
Melieria
Myiomyrmica
Myrmecothea
Notogramma
Otites
Pseudotephritis
Pterocalla
Seioptera
Tetanops
Tetropismenus
Tritoxa
Tujunga
Ulidiotites

ULIDIINAE

Acrosticta
Chaetopsis
Eumetopiella
Euxesta
Homalocephala
Oedopa
**Paroedopa*
Physiphora
**Stenceretma*
Stenomyia
Stictomyia
Texasa
Zacompsia

KEY TO THE GENERA OF OTITIDAE KNOWN TO OCCUR NORTH OF MEXICO

1(2). Sternopleural bristle absent; wing vein r_1 setulose apically; propleural bristle very small; two pairs of scutellar bristles; wing narrow; alula lacking; form antlike; postabdomen of male as in fig. 6 ..... **Myrmecothea** Hendel

2(1). Sternopleural bristle present.
3(4). Anal cell lacking; wings less than 0.25 as wide as long ..... **Steneretma** Loew
4(3). Anal cell present.
5(8). Wings less than 0.33 as wide as long, with but little color pattern; anal cell without extension; propleural bristle very small or lacking; body not metallic; antlike forms.
6(7). Front with narrow but distinct, dull, longitudinal stripe; wings 0.31 as wide as long, *ta* at midlength, color hyaline, with apical dark spot ..... **Cephalia** Meigen
7(6). Front wholly shining; wings 0.25 as wide as long, *ta* at 0.66 of distance from base to apex, color brownish with subapical, transverse, hyaline bar; male postabdomen as in fig. 5 ..... **Myiomyrmica** Steyskal, new genus
(Type, *Cephalia fenestrata* Coquillett)
8(5). Wing at least 0.33 as wide as long, or body metallic-colored (*Eumetopiella*); often with extensive color pattern on wings.
9(22). Anal cell closed apically by straight or outwardly arcuate vein, entirely without point or extension in lower corner; propleural bristle absent or very small.
10(13). Vein r_{2+3} sinuate; r_1 setulose apically; cheeks not over 0.25 of eye height; eye high-oval.
11(12). Costal cell wide, convex anteriorly ..... **Delphinia** R.-D.
12(11). Costal cell narrow, its anterior edge straight ..... **Tritoxa** Loew
13(10). Vein r_{2+3} straight or evenly arcuate; r_1 setulose or bare; eyes roundish.
14(15). One pair of scutellar bristles; r_1 setulose or bare; cheeks more than 0.25 of eye-height; lower occiput tumid, shining; upper parafacials frequently transversely wrinkled; male postabdomen as in fig. 7A ..... **Curranops** Harriot
15(14). Two pairs of scutellar bristles.
16(17). Cheeks less than 0.25 of eye height; hind femora thickened, with middorsal bristle, in male arcuate; r_1 setulose; three dorsocentral bristles ..... **Hiatus** Cresson
17(16). Cheeks 0.25 to 0.33 of eye-height; hind femora not thickened.
18(19). Vein r_1 bare; head not markedly wider than high; front dull; wing as in fig. 14 ..... **Tujunga** Steyskal, new genus
(Type, *Tujunga mackenziei*, new species)
19(18). Vein r_1 setulose; front shining.
20(21). Head much wider than high; *ta* and *tp* separated by more than length of *tp* ..... **Homalocephala** Zett. (*Psairoptera* Wahl.)
21(20). Head approximately as high as wide; *ta* and *tp* approximated, closer together than length of *tp* ..... **Haigia** Steyskal, new genus
(Type, *Haigia nevadana*, new species)
22(9). Anal cell with at least a small point in lower corner; if wholly without point, then propleural bristle well developed.
23(24). Mesopleural bristle lacking (in our species) ..... **Seioptera** Kirby
24(23). Mesopleural bristle present.
25(50). Vein r_1 bare above; r_{2+3} not sinuate.
26(29). Third antennal segment linear, several times longer than wide.
27(28). Vein r_1 not extending nearly to level of *ta*, pterostigma very short; wings plain brown; face protruding between antennae; cheeks less than 0.33 of eye-height; front with strong bristles (fig. 10) ..... **Texasa** Steyskal, new genus
(Type, *Texasa chaetifrons*, new species)
28(27). Vein r_1 extending to level of *ta*, pterostigma much longer than wide; wings with light and dark spots; face not protruding between antennae; cheeks half the eye-height; front with short hairs; male postabdomen as in figs. 11 and 12 ..... **Stictomyia** Bigot
29(26). Third antennal segment not over three times as long as wide.
30(33). Front pitted or strongly wrinkled.[8]
31(32). Vein *sc* forming acute angle with costa; vertex rounded ..... **Acrosticta** Loew
32(31). Vein *sc* approaching costa at almost right angle; vertex acute; male postabdomen as in fig. 16 ..... **Notogramma** Loew
33(30). Front smooth or only slightly pitted at bases of hairs.
34(39). Face convex in middle; epistoma somewhat retreating; heavily pale-pruinose species; head not longer than high.
35(36). Wings not at all spotted; face with neither bar nor spot; wing, head, and male postabdomen as in fig 8 ..... **Ulidiotites** Steyskal, new genus
(Type, *Ulidiotites dakotana*, new species)
36(35). Wings with a few spots anteroapically.
37(38). *Ta* biangulate; face with brown bar across middle ..... **Oedopa** Loew
38(37). *Ta* straight; face with central black spot ..... **Paroedopa** Coquillett
39(34). Face straight to concave.
40(41). Head nearly twice as long as high ..... **Eumetopiella** Hendel
41(40). Head at most a little longer than high.
42(45). Third antennal segment with upper apex angulate or pointed; medifrons with a few pairs of cruciate bristles or face strongly retreating.
43(44). Front with distinct series of converging bristles that are much stronger than surrounding hairs; apical angle of anal cell prolonged; face but little retreating, epistoma somewhat prominent ..... **Chaetopsis** Loew
44(43). Front with all hairs and bristles subequal and proclinate; apical angle of anal cell acute but not prolonged; face distinctly retreating; epistoma not prominent ..... **Stenomyia** Loew
45(42). Third antennal segment rounded above, if somewhat angulate then medifrons with many scattered setulae or bristles; *ta* near or beyond middle of discal cell.
46(47). Medifrons bare, in upper part with four low, longitudinal swellings; cell R_5 usually closed or nearly so; aedeagus with specialized tip ..... **Physiphora** Fallén (*Chrysomyza* Fallén)
47(46). Medifrons with hairs or bristles.
48(49). Front 1.5 times as wide as an eye; body not metallic; prescutellar bristles absent ..... **Zacompsia** Coquillett
49(48). Front at most as wide as an eye; body color metallic; prescutellar bristles present ..... **Euxesta** Loew
50(25). Vein r_1 with at least a few hairs above apically; if bare, r_{2+3} sinuate.
51(64). One or more of the following characters present: stigma enlarged; r_{2+3} sinuate; anal cell with long extension. (Propleural bristle small or lacking in this group.)
52(57). *Ta* and *tp* running parallel and so obliquely placed that *tp* forms a right or obtuse angle with m_1.
53(54). Tip of anal cell with long extension; five pairs of *dc* and *acr* ..... **Dyscrasis** Aldrich
54(53). Tip of anal cell not produced; one pair of *dc* (cf. also rubrics 11, 12, and 19).

[8] *Ulidia* comes here. Several North American species have been referred to *Ulidia*, but all of them must be assigned elsewhere.

55(56). Costal cell broad, convex anteriorly ..... **Delphinia** R-D.
56(55). Costal cell narrow, its anterior edge straight ..... **Tritoxa** Loew
57(52). *Ta* and *tp* not parallel, *tp* forming an acute angle with m_1.
58(63). Extension of anal cell as long as cell proper.
59(60). Fore and hind margins of wing not parallel; cell R_5 straight ..... **Callopistromyia** Hendel
60(59). Fore and hind margins of wing parallel.
61(62). Vein r_{2+3} straight; brown pattern of wings consisting of broad costal margin; male postabdomen as in fig. 9 ..... **Diacrita** Gerstaecker
62(61). Vein r_{2+3} sinuate (except in *P. strigula*); brown pattern covering middle of wing ..... **Pterocalla** Rondani
63(58). Extension of anal cell much shorter than cell proper; arista bare or pubescent; head roundish; third antennal segment almost circular ..... **Pseudotephritis** Johnson
64(51). None of the following characters present: large stigma; r_{2+3} strongly sinuate; anal cell with long extension. (Propleural bristle well developed, except in *Idana, Tetanops,* and *Tetropismenus.*)
65(74). Cheeks less than 0.33 as high as eye; parafacials and parafrontals never wrinkled; two (or abnormally three) pairs of scutellar bristles.
66(67). Frontal index[7] 1.4; two *dc*; propleural bristle strong; small species, less than 4.0 mm. long; in North American species with *ta* and *tp* seldom separated by more than length of *tp* and with dark fascia covering both *ta* and *tp*; anal cell lacking point in lower corner ..... **Herina** R.-D. (*Tephronota* Loew)
67(66). Frontal index not more than 1.2; larger forms.
68(69). Thorax with presutural *dc*, altogether five or six pairs; propleural bristle strong; pruinose forms with spotted wings ..... **Melieria** R-D.
69(68). Only one or two pairs of *dc*, none presutural.
70(71). Wings with extensive dark pattern not consisting of spots; thorax and abdomen black, with yellow-pruinose bands; propleural bristle absent or very small; male postabdomen as in fig. 4 ..... **Idana** Loew
71(70). Wings with but little pattern or with one of spots; thorax without contrasty pattern; propleural bristle usually well developed.
72(73). Wings at most with short band and apical spot or subbasal spot only; third antennal segment rounded apically or slightly angulate ..... **Otites** Latr. (*Ortalimyia* Curran)
73(72). Wings with spots, including one over each crossvein; third antennal segment curved, with sharply pointed tip ..... **Ceroxys Macq.** (*Anacampta* Loew)
74(65). Cheeks more than 0.33 as high as eye; parafacials and parafrontals frequently wrinkled; frontal index less than 1.2; propleural bristle small or lacking.
75(76). Three or four pairs of *sc;* all hairs long; orbits smooth; head largely yellowish; antennae very short and black ..... **Tetropismenus** Loew (*Califortalis* Curran)
76(75). Two (or abnormally three) pairs of *sc*; hairs and bristles short ..... **Tetanops** Fallén

Subgenera of *Tetanops:*

a. Front dull, without round bare spots ..... **Psaeropterella** Hendel, status nov.
a'. Front shining or dull; if dull, with round bare spots; usually with one or more grooves laterad of antennae.
b. Front wholly shining, usually distinctly wrinkled medially and along orbits ..... **Eurycephalomyia** Hendel, status nov.
b'. Front pruinose, at least posterolaterally, and with round bare spots ..... **Tetanops** s. str.

[7] Frontal index = length of front from anterior ocellus divided by narrowest width of front (here at level of anterior ocellus).

DESCRIPTIONS OF NEW GENERA AND SPECIES

Genus **Tujunga** Steyskal, novum

An otitine distinguished as in the foregoing key, by the following salient characters: sternopleural and mesopleural bristles present; propleural bristle minute; wing 0.38 as wide as long, without color pattern; anal cell closed by almost straight crossvein, without point in lower corner; vein r_1 bare; vein r_{2+3} nearly straight; two pairs of scutellar bristles; cheeks 0.33 of eye-height; head slightly higher than wide; front dull; hind femora not thickened.

The name is taken from the type locality and is of feminine gender. The genus apparently is related to *Hiatus, Curranops, Tetanops,* and *Tetropismenus.* Type of genus, the following new species.

Tujunga mackenziei Steyskal, sp. nova
(Fig. 14)

Male.—Length of wing 3.1 mm. Color black to brown, moderately yellowish-gray pruinose, especially on dorsum of thorax and back of head; wings smoky brown; halteres dark yellow; hairs and bristles black; squamal cilia yellow; antennae black; arista dark brown.

Head a little higher than long, about 0.25 wider than thorax; antennae well separated, third segment a little longer than broad; arista finely pubescent, 0.33 mm. long, swollen at base; face gently concave in profile, with deep antennal grooves; front flat, dull, velvety, 0.4 of width of head, index 1.0, parallel-sided, with many coarse hairs; cheeks wrinkled, 0.33 of eye-height; eyes nearly round; bristles long, consisting of 1 *oc*, 1 *poc*, 1 *vte*, 1 *vti*, 2 *fo* placed rather closely together, the posterior one only slightly forward of anterior ocellus.

Thorax approximately as wide as long; scutellum half as long as wide, convex above, bare except for two pairs of bristles, the apical pair rather close together and convergent apically, the laterals about halfway between the apicals and base of scutellum; chaetotaxy: *ppl* minute, 1 *stpl*, 1 *h*, 2 *ntpl*, 2 *sa*, 2 *pa*, 1 *dc*, ? *acr*; prosternum and pteropleura bare; mesopleura and mesonotum covered with coarse hairs.

Legs of ordinary type, femora moderately developed, anterior femora with ventral and posterior bristles approximately as long as femoral diameter.

Wings as in fig. 14; vein r_1 bare; anal cell truncate, without point in lower corner.

Preabdomen with lengths of tergites as follows: 1-2 (syntergite), 0.6 mm.; 3, 0.2 mm.; 4, 0.27 mm.; 5, 0.39 mm. Tergites 1-4 dull, minutely rugulose; tergite 5 coarsely and deeply, irregularly, transversely rugose.

Postabdomen shining; aedeagus slender, tapering to simple tip, with short bristles in proximal half, except close to base. (The abdomen has not been dissected).

Female.—Similar to male. Color somewhat paler; humeri, face, and base of femora light brown; length of wing 3.45 to 3.7 mm.; abdomen with preabdominal tergites subshining, very minutely rugulose; length of tergite uncertain because of shrunken condition, but apparently of following lengths: 1-2, 0.6 mm.; 3, 4, and 5, 0.3 mm. each; 6, 0.2 mm.; ovipositor sheath shining, strongly tapering, approximately 1.0 mm. long; ovipositor not exserted, tip apparently quite narrow.

Types.—Holotype (♂), allotype (♀), and one paratype (♀), Tujunga Canyon, Los Angeles County, California, Jan. 22, 1947 (G. P. MacKenzie); one paratype (♀), East Highlands (? near San Bernardino), California, II-15; all in United States National Museum collections.

I am happy to dedicate this species to its collector, who supplied me with many fine specimens of Diptera in years past.

Genus **Haigia** Steyskal, novum

An otitine distinguished as in the foregoing key, by the following salient characters: sternopleural and mesopleural bristles present; propleural bristle minute; wing 0.37 as wide as long, with well-developed color pattern; vein r_1 setulose from end to stem vein; r_{2+3} almost straight; *ta* and *tp* approximated, separated by less than length of *tp;* anal cell closed by almost straight crossvein, without point in lower corner; two pairs of scutellar bristles; cheeks 0.25 of eye-height; head only slightly wider than high; front shining, index 1.1; hind femora not thickened.

The genus is dedicated to the collector of its type species, in token of his prowess. The name is of feminine gender.

The relationships apparently are with *Homalocephala, Tritoxa,* and *Idana.* Type of genus, the following new species.

Haigia nevadana Steyskal, sp. nova
(Fig. 15)

Male.—Length of wing 2.55 to 3.0 mm. Color blackish, except the following brownish-yellow parts: face and cheeks; antennae; palpi; humeri; supraalar areas; scutellum; pteropleura; sides of metanotum; prosternum; legs, except apical tarsal segments and sometimes fore and hind tibiae. Middle and anterior front also sometimes brown. Halteres and squamae, including cilia, whitish. Bristles and hairs black.

Head as in figure 15D; smooth and shining, except narrow, white-pruinose frontal, facial, and genal orbits and antennal grooves; 0.15 wider than thorax; cheeks 0.25 of eye-height; front 0.43 of width of head, index 1.1, slightly concave above; bristles: 1 *oc,* 1 *poc,* 1 *vte,* 1 *vti, 2 fo;* arista bare, brown except yellow extreme base.

Thorax about as long as wide; scutellum half as long as wide; mesonotum lightly brownish-pruinose; sternopleura and lower propleura white-pruinose; chaetotaxy; *ppl* minute, 1 *mspl,* 1 *stpl,* 1 *h, 2 ntpl,* 1 *sa, 2 pa,* 1 small *dc,* 1 much larger *acr* (*prsc*); *2 sc.*

Wings as in figure 15A, hyaline, with brown costal cell, stigma, apical spot, area around fork of *rs,* band from stigma to posterior end of *ta,* and spot in middle of first basal cell; r_1 setulose from end to stem vein; anal cell truncate, without point or extension.

Legs of ordinary form; slender; fore femora with a few long dorsal, posterior, and ventral bristles in apical half; hind femora with a few small posterodorsal, subapical bristles.

Preabdomen subshining, very minutely and shallowly shagreened, with sparse, short hairs. Postabdomen black, as in figures 10B and 10C; aedeagus long, bristled on nearly entire length, with saccate, pilose tip; surstyli clawlike, mesially with a row of denticles which are continued two-thirds of way down a pair of wedge-shaped strips on ventral side of epandrium.

Female.—Similar to male. Length of wing 2.7 to 3.1 mm. Ovipositor sheath finely, transversely striate; ovipositor very slender.

Types.—Holotype (♂), allotype (♀), paratypes (*22* ♂♂, *26* ♀♀), Winnemucca, Humboldt County, Nevada, May 27, 1960 (T. R. Haig), taken in evening on plants of sagebrush, *Artemisia tridentata.* Types and 10 paratypes in United States National Museum collections, five paratypes retained by me, the remainder returned to Bureau of Entomology, California State Department of Agriculture.

Genus **Ulidiotites** Steyskal, novum

An otitine distinguished as in the foregoing key, by the following salient characters: sternopleural and mesopleural bristles present; propleural bristle minute; anal cell of wing with well-developed extension in lower corner; vein r_1 bare; r_{2+3} not sinuate; wing 0.38 as wide as long, without spots or other color pattern; scutellum with two pairs of bristles; cheeks nearly half the eye-height; head not wider nor longer than high; front tumid, broadened anteriorly, smooth, dull; third segment of antennae ovoid, less than twice as long as wide.

The name is a compound of two generic names, *Ulidia* and *Otites,* and is of the same gender as *Otites,* feminine. The genus apparently is related to *Oedopa* and *Paroedopa.* Type of genus, the following new species.

Ulidiotites dakotana Steyskal, sp. nova
(Fig. 8)

Male.—Length of wing 2.8 to 3.2 mm. Color yellow, everywhere covered with strong, whitish to yellowish pruinosity under which the blackish color of the thoracic dorsum, sternum, abdomen, ocellar triangle, and central occiput is faintly perceptible.

Bristles and hairs black, only the short squamal cilia, the hairs of the proboscis, and a pair of hairs at the end of the last segment of the tarsi yellow. Wings whitish; veins brownish, except yellowish costa (as far as end of r_2), *sc*, r_1, basal half of r_2, and base of *m*. Squamae, their cilia, and halteres pale yellow.

Head as in figure 8B, about 0.2 wider than thorax. Front tumid and widened anteriorly; frontal index 0.9; width of front at level of anterior ocellus half the total width of head; face convex, with distinct antennal grooves; cheeks almost half of eye-height; antennae widely separated; arista bare, blackish, except swollen, yellow, basal part; bristles: 1 small *oc*, 1 small *fo*, 1 each moderately large *vte* and *vti*, 1 small *poc*.

Thorax approximately as long as wide; scutellum flattened above, a little more than half as long as wide; chaetotaxy: 1 *stpl*, 2 *mspl*, 1 very small *ppl*, 1 *h*, 2 *ntpl*, 1 *sa*, 2 *pa*; 8 or 9 small *dc*, decreasing in length anteriorly; 2 *sc*, the apical pair convergent apically, a little closer to each other than to lateral pair; middle of propleura with a few yellow hairs, none on prosternum or pteropleura.

Legs with short but rather stout setulae; anterior femora with short but complete rows of posterodorsal and posteroventral bristles; hind femora with three short anteroventral bristles in apical half; all femora swollen, about twice as thick as tibiae.

Wings as in figure 8A; vein r_1 bare; anal cell with well-developed extension in lower corner; first posterior cell strongly narrowed apically.

Abdomen with four apparent preabdominal segments of nearly equal length, smooth, with sparse setulae; postabdomen as in figure 8C, aedeagus distinctly bristled except near base, aedeagal apodeme slender, Y-shaped.

Female.—Similar to male; length of wing 3.7 mm.; all bristles somewhat longer and heavier; penultimate preabdominal segment (sixth) half as long as ultimate or antepenultimate segments; ovipositor dark brown, acute, slightly downwardly curved.

Types.—Holotypes (♂) and one paratype (♂), Martin, Bennett County, South Dakota, July 6, 1924 (H); two paratypes (♂), same locality, July 7, 1924 (H); allotype (♀) and one paratype (♂), Sheridan County, Nebraska, June 5, 1956 (R. and K. Dreisbach). The Nebraska specimens were taken in the southwest corner of Sheridan County, about 90 miles from Martin, South Dakota. The types are in the United States National Museum collections, except one paratype from each locality which are in the Dreisbach collection, Midland, Michigan.

Genus **Texasa,** Steyskal, novum

A ulidiine distinguished as in the foregoing key, by the following salient characters: sternopleural and mesopleural bristles present; propleural bristle lacking; anal cell of wing with distinct, but short, extension in lower corner; vein r_1 bare, ending well short of level of *ta*; r_{2+3} evenly arcuate; wing 0.41 as wide as long, without spots or distinct color pattern; two pairs of scutellar bristles; cheeks less than 0.33 of eye-height; face protruding between antennae, strongly retreating; third antennal segment several times longer than wide; front with strong bristle.

The name is derived from that of the State of Texas, and is of feminine gender. The genus apparently is related to *Stictomyia*. Type of genus, the following new species.

Texasa chaetifrons Steyskal, sp. nova
(Fig. 10)

Male.—Length of wing 2.7 mm. Color black, with dull green and brassy metallic reflections; front, parafacials, and cheeks dark brown; palpi (except extreme tip), arista, and tarsi yellowish; wings dark brown, costal margin darker; squamae and their cilia dark brown; halteres blackish; all bristles black.

Head as in figure 10B, the cross-hatched areas white-pruinose, otherwise shining; front 0.5 mm. wide at level of ocellar bristles; frontal triangle extending halfway from anterior ocellus to frontal margin; third antennal segment with black pubescence; front with rather irregularly disposed bristles and bristly hairs, in anterior view not as seriate as they appear in side view.

Thorax a little broader than long; chaetotaxy: 0 *ppl*, 1 *mspl*, 1 *stpl*, 1 *h*, 2 *ntpl*, 1 *sa*, 1 *pa*, 1 (or more?) *dc*, 2 *sc*; mesopleura with many bristly hairs; pteropleura bare.

Legs without well-developed bristles; femora moderately thick.

Wings as in figure 10A; 0.41 as wide as long; all veins bare; vein r_{2+3} long and evenly arcuate.

Abdomen with coarse setae; postabdomen as in figure 10C, aedeagus slender, bare, tip slightly expanded; aedeagal apodeme a two-pronged fork; epiphallus C-shaped; claspers (surstyli) clawlike.

Female.—Unknown.

Type.—Holotype (♂), Forestburg, Montague County, Texas, mid-May 1942 (L. H. Bridwell), in United States National Museum.

NEW SYNONYMY

Genus **Tetropismenus** Loew

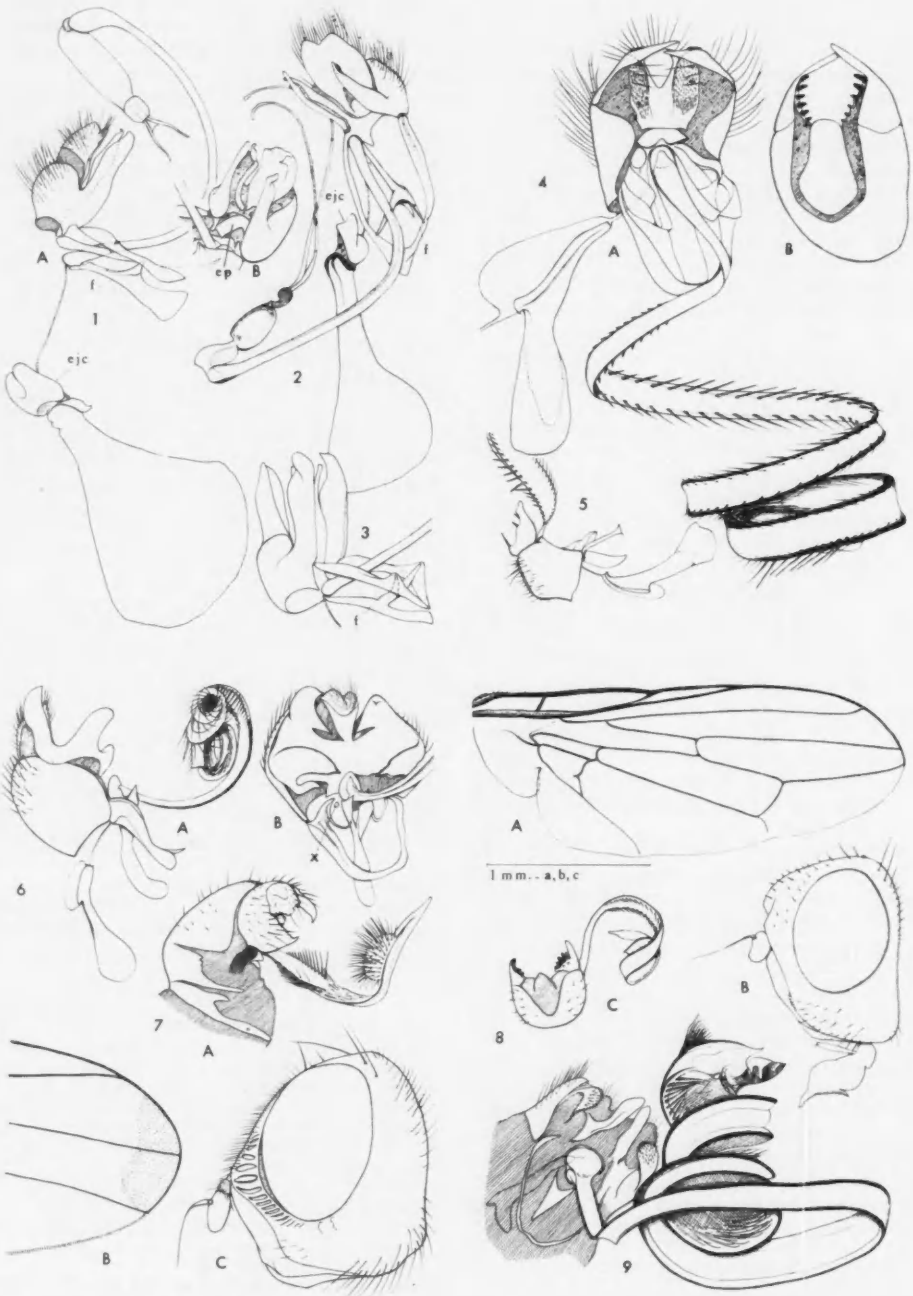
Tetropismenus Loew, 1876, Zeitschr, ges. Naturwiss. 48: 333; type *T. hirtus* Loew, by monotypy.
Califortalis Curran, 1934, Fam. and Gen. N. Amer. Dipt.: 284; type, by original designation, *C. hirsutifrons* Curran, l. c. (nomen nudum). **New synonymy.**

The descriptions show that these names are obviously synonymous.

Genus **Otites** Latreille

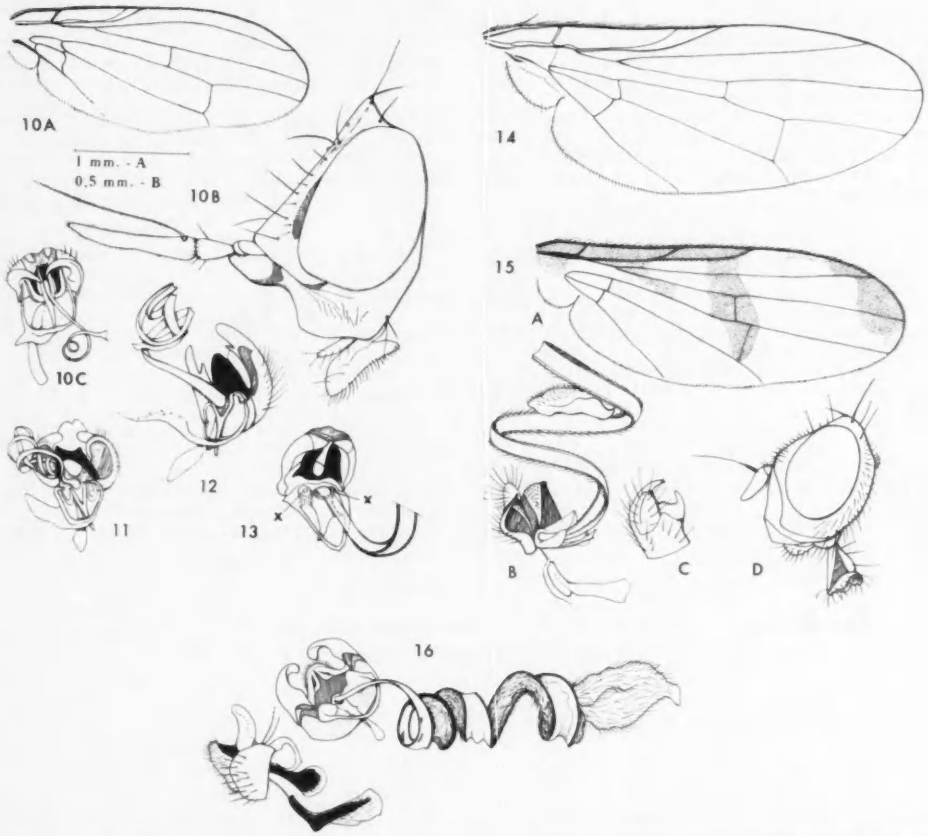
Otites Latreille, 1804, Nouv. Dist. Hist. Nat. 24: 196; type, by subsequent monotypy, *O. elegans* Latreille (=*Musca formosa* Panzer).
Ortalimyia Curran, 1934, Fam. and Gen. N. Amer. Diptera: 284; type, by original designation, *Ortalis snowi* Cresson. **New synonymy.**

Since *Ortalis snowi* and the several other North American species fit quite well with the European species placed in *Otites*, it is difficult and unnecessary to maintain a distinct genus for our forms.



FIGS. 1-3.—Andria of male Platystomatidae. 1A. *Senopterina brevipes* (Fabr.), sinistral view; 1B, same, anterodextral view. 2, *Pogonortalis doclea* (Walker), anterodextral view. 3, *Rivellia variabilis* Loew, anterosinistral view less terminal part of aedeagus and ejaculatory apodeme. *ejc*, ejaculatory cap; *ep*, epiphallus; *f*, fultella (aedeagal apodeme, phallodeme).

(Balance of legends on foot of opposite page).



FIGS. 10-13.—Details of male Ulidiinae. 10A, *Texasa chaetifrons*, n. sp., wing; 10B, same, head; 10C, same, andrium, anterior view. 11, *Stictomyia longicornis* Bigot, andrium, anterodextral view. 12, *Stictomyia punctata* Coquillett, andrium, anterodextral view. 13, *Physiphora demandata* (Fabr.), andrium, anterodextral view less terminal part of aedeagus and ejaculatory apodeme (*x*, rudiment of pregonite ?). The epiphallus is shown in solid black in figs. 10C, 11, 12, and 13.

FIGS. 14-15.—Details of male Otitinae. 14. *Tujunga mackenziei*, n. sp., wing. 15A, *Haigia nevadana*, n. sp., wing; 15B, same, andrium, anterosinistral view; 15C, same, epandrium and proctiger, posterosinistral view; 15D, same, head.

FIG. 16.—Andrium of *Notogramma cimiciformis* Loew.

FIGS. 4-5.—Andria of male Otitinae. 4A, *Idana marginata* Say, anterodextral view; 4B, same, posterodextral view of epandrium and proetiger. 5, *Myiomyrmica fenestrata* (Coquillet), sinistral view less terminal part of the aedeagus.

FIGS. 6-7.—Details of male Otitinae. 6A, *Myrmecothea myrmecoides* (Loew), sinistral view; 6B, same, anterosinistral view less terminal part of aedeagus and ejaculatory apodeme (*x*, rudiment of pregonite ?). 7A, *Curranops apicalis* (Cole), postabdomen, sinistral view; 7B, same, tip of wing; 7C, same, head.

FIGS. 8-9.—Details of male Otitinae. 8A, *Utidiotites dakotana*, n. sp., wing; 8B, same, head; 8C, same postabdomen, posterior view. 9, *Diacrita costalis* Gerstaecker, andrium, anterosinistral view.

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The Presence of 2-Hexenal in the Scent Gland of the Pentatomid *Brochymena quadripustulata*[1]

MURRAY S. BLUM

Department of Entomology, Louisiana State University, Baton Rouge

ABSTRACT

The scent gland of the pentatomid *Brochymena quadripustulata* (F.) contains a single volatile compound. By means of infrared spectroscopy, mass spectrometric analysis, vapor-phase chromatography and the preparation of a 2,4-dinitrophenylhydrazone derivative, this compound has been identified as the *trans* form of 2-hexenal. Experiments using two ant species as predators indicate that the ejection of this compound by *Brochymena* is employed as a defensive mechanism.

The tribe Halyini of the family Pentatomidae is represented in the United States by the single genus *Brochymena*. These bugs are frequently found on trees and consequently are known as tree bugs. In Louisiana, *Brochymena quadripustulata* (F.) is frequently found on crape myrtle in the early summer when the tree is shedding its bark. Adults of this bug are found either under the shedding bark on the trunk or on the lower branches. This species has been reported to prey on the tussock and brown-tail moths (Sanderson 1904), and Brimley (1907) has reported that it attacked the new growth on apple trees.

When approached or disturbed, this pentatomid ejects a pungent liquid. This highly organoleptic material, which is stored in the scent gland, has been identified as the *trans* form of the carbonyl compound 2-hexenal. In addition, experiments with two ant species have demonstrated that *Brochymena* ejects this compound accurately toward potential predators and that the spray has a repellent function.

MATERIALS AND METHODS

Male and female adults of *Brochymena* were collected on crape myrtle and were kept at 60° F. along with sprigs of crape myrtle and water.

The scent-gland secretion was collected by removing the abdominal and thoracic dorsa and piercing with fine capillaries the red, scalloped scent gland which lies on the floor of the body cavity in the metathoracic and first abdominal segments. The scent-gland secretion first was characterized by infrared, mass spectroscopic and vapor phase chromatographic analyses.

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Infrared examinations were made on a Perkin-Elmer Model 21 spectrograph, in a carbon tetrachloride solution.

For mass spectroscopic analyses, 0.5 μl samples were injected into the heated inlet (100° C.) of a modified Consolidated 21-102 analytic mass spectrometer employing a normal magnet run at a pressure of 51.05μ.

Vapor phase chromatographic analyses were performed on a Perkin-Elmer Model 154B vapor phase chromatograph by injecting 0.5 μl samples into the instrument inlet. Ucon® nonpolar lubricant[2] was employed at a temperature of 150° C. and a helium flow rate of 50 cc/min.

A 2,4-dinitrophenylhydrazone derivative was prepared from the clear, yellow fluid collected in the capillaries by adding the scent-gland fluid to a saturated solution of 2,4-dinitrophenylhydrazine in 2N HCl. The solution was cooled at 0° C. for 1 hour, after which the precipitate was separated by filtration. The 2,4-dinitrophenylhydrazone was recrystallized twice from methanol-water (3:1) and was dried over P_2O_5.

The spray mechanism of *Brochymena* was studied by placing bugs on filter papers which had been treated with an alcoholic solution of 2,4-dinitrophenylhydrazine. The ejected carbonyl compound appeared as bright orange spots on the yellow papers. Repellency tests were made by placing the bugs on treated papers which were placed near colonies of the imported fire ant *Solenopsis saevissima* v. *richteri* Forel or the Texas harvester *Pogonomyrmex barbatus* (F. Smith).

RESULTS

The infrared spectrum of the fluid in the scent gland of *Brochymena* demonstrated that a carbonyl compound was present. Strong absorption at 5.89μ in combination with a band at 3.66μ indicated that an aldehydic compound was present which contained unsaturation (6.08μ) of the *trans* form as demonstrated by the strong band at 10.25μ.

The mass spectroscopic fragmentation pattern is shown in table 1. The parent mass was 98. The pattern indicated that the *Brochymena* secretion was a hexenal. Comparison of the pattern of the bug secretion with synthetic 2-hexenal demonstrated that the fragmentation patterns were identical (table 1).

Analysis of the *Brochymena* scent-gland fluid on the vapor phase chromatograph showed that only one volatile component was present. This compound had the same retention time as synthetic 2-hexenal.

The 2,4-dinitrophenylhydrazone prepared from the scent gland fluid consisted of red-orange needles melting at 143°-144.5° C. and did not produce a melting point depression in admixture with the same derivative of synthetic 2-hexenal melting at 145°-146° C. The elementary analysis of the *Brochymena* derivative corresponded to a hexenal (calculated for $C_{12}H_{14}N_4O_4$: C, 51.70; H, 5.01; N, 20.04. found: C, 51.50; H, 5.17; N, 19.90).

Table 1.—Mass spectrometric analysis of the scent gland secretion of *Brochymena quadripustulata* (F.).

Mass/charge	*Actual Divisions of Spectrum* *Brochymena* secretion	Synthetic 2-hexenal	Residual
27	479.2	479.1	+0.1
28	299.0	299.0	0
29	465.3	465.2	+0.1
39	484.0	484.1	−0.1
41	658.8	658.7	+0.1
42	380.0	380.0	0
43	125.5	125.4	+0.1
55	412.4	412.3	+0.1
57	235.2	235.2	0
69	295.8	295.9	−0.1
70	80.7	80.7	0
83	255.1	255.0	+0.1
97	45.3	45.3	0
98	100.4[a]	100.4[a]	0

[a] Parent mass.

The infrared spectrum of synthetic 2-hexenal was identical to that of the *Brochymena* secretion.

The spray mechanism and the repellent function of the Brochymena secretion.—After being placed on filter papers impregnated with 2,4-dinitrophenylhydrazine, the carbonyl compound ejected by *Brochymena* was easily detected as an orange spot. Irritating the dorsum of *Brochymena* with a probe caused a bilateral ejection, sometimes to a distance of 6 inches or more. However, if the legs on one side were stimulated, the ejection was always unilateral to the stimulated side. When a leg was stimulated, *Brochymena* would often eject repetitive discharges which would continue for up to 30 seconds, even when the insect was walking. The material was ejected as small droplets rather than a fine spray.

When *Brochymena* was placed near a colony of *Pogonomyrmex barbatus* (F. Smith), the repellent action of the spray was clearly indicated. In a typical encounter, individual *Pogonomyrmex* workers would attack *Brochymena* by grasping a leg with their mandibles. *Brochymena* immediately ejected at the ant and only on the side under attack. The ant would rapidly withdraw, indicating by its abnormal walking movement an apparent state of irritation. The ant would perform cleansing movements for a considerable length of time after its encounter with the bug. Except for three individuals whose scent-gland secretion had been exhausted by previous mechanical stimulation, no specimen of *Brochymena* was injured in any of the 23 encounters observed.

Bugs which were placed near a colony of the imported fire ant *Solenopsis saevissima* v. *richteri* Forel were often attacked simultaneously by as many as six ants. The encounters frequently resulted in ants grasping the legs on both sides of the body, whereupon *Brochymena* would discharge bilaterally and often repetitively at the ants. Exhibiting apparent seizures as they moved, the sprayed ants immediately

[2] Substituted polyethylene glycol; Union Carbide and Chemicals, New York, N. Y.

withdrew leaving a streak on the paper from the secretion on their bodies. For as much as a minute after the discharge, *Brochymena* was immune from further attacks by ant workers who, often before physical contact was made, withdrew from the area of the freshly discharged bug. This immunity is probably attributable to the fact that some of the ejected carbonyl was still on the bug's body, as was demonstrated by the orange streaking of the treated filter paper when the bug moved from the field of the encounter. On the other hand, *Brochymena* was readily attacked by *Solenopsis* if the paired ostioles through which the spray is discharged were sealed with embedding wax.

DISCUSSION

The occurrence of 2-hexenal as the only volatile compound in the scent gland of *Brochymena* is in marked contrast to the chemistry of the scent gland of another pentatomid, *Oebalus pugnax* (F.). In the latter, the principal carbonyl compound is 2-heptenal. In addition, the hydrocarbon *n*-tridecane as well as other carbonyl compounds are present (Blum et al. 1960). *Brochymena* is a member of the tribe Halyini and *Oebalus* of the tribe Pentatomini. These two pentatomids are not closely related and it is not surprising that the gross chemistry of the scent gland of *Oebalus* is considerably more complex than that of *Brochymena*. The fact that the principal aldehydes in the two species differ by only one carbon atom may have evolutionary significance.

2-Hexenal has also been found in the cockroach *Eurycotis floridana* (Walker) (Roth et al. 1956). In the plant kingdom this volatile carbonyl compound has been found in many plant tissues. 2-Hexenal is one of the principal carbonyls found in strawberries (Dimick and McKower 1956), leaves of the Chinese "tree of heaven" (Nye and Spoehr 1943), and apple juice (White 1950).

Certainly, *Brochymena* employs 2-hexenal to repel some insect species. The ability of this pentatomid to direct its spray in the direction of stimulation indicates the defensive value of the spray. 2-Hexenal, although an obvious irritant to both *Pogonomyrmex* and *Solenopsis* workers, did not produce mortality among the exposed ants. Similarly Eisner (1958) reported that the spray of the carabid *Brachymus ballistarius* Lec. was repellent to several insect species and to a spider. This spray, which is quinoid in nature, irritated the exposed predators and caused seizures in both ants and carabids.

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Effects of Parental Age on the Life Cycle of *Drosophila melanogaster*[1]

DENNIS M. O'BRIAN[2]

Department of Biology, Fordham University, New York

ABSTRACT

Effects of parental age were followed through nine successive generations, reared at 25° C., for offspring from young, middle-aged, and old parents. The reproductive capacity of offspring from middle-aged flies was initially lower than that of the parental generation, while that of off-spring from old (and also, usually, from young) parents was higher. The offspring from young parents produced viable eggs for a longer period (46 days, increasing to 51 days in the last three generations) than did the parental generation (41 days); for offspring from middle-aged parents this period was greater initially (46 days) but dropped to 31 days in the last three generations; with offspring from old parents production of viable eggs always had a shorter duration than in the parental generation and reached a minimum of 25 days. In general, offspring from middle-aged and those from old flies had a shorter life span than that of the parental generation; this aging effect was obtained in the first generation.

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[2] Present address: Department of Biology, Seton Hall University, South Orange, New Jersey.

The effects of parental age on offspring have been reported by various investigators. Comfort (1953) noted that there was no significant change in the longevity of *Drosophila subobscura* Col., when obtained through successive generations from old parents. Goetsch (1956) reported that descendents from young *Drosophila melanogaster* Meig. lived longer than those from old flies. Rockstein (1957) showed that in the house fly, *Musca domestica* L., the female had a greater longevity when derived from young than from old parents, but parental age had no effect on male survival. However, this investigator (1959) later noted that males derived from old had a greater longevity than those from young parents.

Ludwig (1956) observed that in the mealworm, *Tenebrio molitor* L., the duration of larval life diminished in the progeny from old as compared with those from young beetles. Tracey (1958), using the same species, found significant differences between offspring from young and from old parents, those from the latter having a shorter life and a higher growth rate. Ludwig and Fiore (1960) noted that the aging effect on the larvae of this species was not evident until 1 month following the emergence of the parents, and on the duration of adult life until at least 7 weeks following emergence. On the other hand, Fiore (1960) observed in the dark mealworm, *T. obscurus* F., that there were no consistent effects on the duration of the life cycle due to parental age. However, larvae from old had a slower rate of growth than those from young parents and failed to attain the same maximal weight.

In view of these experiments and the scarcity of work on parental age effects in *Drosophila melanogaster*, this work was undertaken to determine whether parental age has effects on the longevity of the offspring and on the fecundity as measured by duration of the viable egg laying period, and the number of offspring produced per individual. This investigation was followed through nine successive generations, in each case selecting offspring from young, middle-aged, and old parents.

MATERIALS AND METHODS

All cultures were maintained in an incubator at 25° C. *Drosophila melanogaster* (Oregon strain R), was inbred for twelve generations to obtain a uniform stock. Adults of various ages from this stock were placed in fresh culture bottles, and eggs were collected for a period of 48 hours. Thus the adults which emerged during the first 48 hours from these eggs were young from parents of various ages. Eggs were collected from these young adults during the first 48 hours of the egg-laying period. The adults which emerged during the first 48 hours from this collection were used to set up the parental generation. The number of adults obtained during each 24-hour collection period was recorded. However, in timing the egg collecting periods, since the preoviposition period is 48 hours, the age of the parents was calculated from the beginning of egg laying rather than from emergence. From this parental stock, eggs were collected when the flies were 0-2 and 15-16 days old, and from the last 24-hour period which yielded viable eggs. With this exception, parental age is calculated on the basis of days following emergence. The adults which emerged during the first 48 hours from these egg collections were used to set up the stocks, offspring from young, middle-aged, and old parents.

Offspring from young parents were always obtained during the first 48 hours following adult emergence. Those from middle-aged parents were collected during the 15-16 day period, and those from old parents during the last 24-hour period of viable egg production. The number of adults obtained during each 24-hour period was recorded and their average survival in days was calculated on the basis of days following emergence. This method of obtaining material was followed for each successive generation through nine generations.

Eggs were collected from the young parental stocks at 0-2, 2-3, 6-7, 12-13, 18-19, 24-25, 30-31, 35-36, 40-41, 45-46, and 50-51 days. Those from middle-aged and old stocks were collected at the same ages, as long as viable eggs could be obtained. The number of offspring per female was calculated for each of these periods by counting the number of adults which emerged from each group and dividing by the number of surviving females at the time of egg production. However, for the 0-2 day period the offspring per female was calculated differently because of the 48-hour preoviposition period. In this collection period, eggs were laid by flies which had emerged during the first 24 hours. The number of offspring per female for this group was obtained by counting the number of adults which emerged and dividing by the number of females which were obtained during the first 24-hour period.

Records were obtained of the time required from egg collection to puparium formation, to first adult emergence, and of the number of adults which emerged. This latter figure was obtained by counting the number which emerged during 24-hour intervals following the appearance of the first adult. When no flies emerged during a 3-day period following the first emergence, the experiment was concluded.

The flies were transferred to fresh culture bottles at the beginning and at the end of each egg collecting period, and as a result they were never in any one culture bottle for longer than 5 days. To avoid overcrowding, the number was usually less than 55 per half-pint milk bottle. However, in two cases there were 61, and in one case there were 58.

Throughout this experiment a cornmeal-molasses culture medium was used. Dowicide® solution (10% in 95% ethyl alcohol) was added during preparation of the medium as a mold inhibitor.

OBSERVATIONS

The age of the parents had no effect on the duration of the preimaginal stages.

In calculating the reproductive capacity and the duration of the viable egg laying period, the results are listed in three groups to show the effects more clearly. Group I comprises generations F_1, F_2, and F_3; II, F_4, F_5, and F_6; and III, F_7, F_8, and F_9.

In table 1 are shown the number of females used in each group at each parental age. The females collected during the first 24 hours laid the eggs for the 0-2 day egg-collection period listed in table 2.

Table 1.—The number of female and male flies collected during the 48 hours following the first emergence. Group I consists of generations F_1, F_2, and F_3; Group II, F_4, F_5, and F_6; Group III, F_7, F_8, and F_9.

	First 24-hour collection		Second 24-hour collection	
	Female	Male	Female	Male
Parental generation				
Control	87	46	56	68
Offspring from young parents				
Group I	64	40	49	42
Group II	66	34	60	52
Group III	84	44	51	53
Offspring from middle-aged parents				
Group I	225	156	76	109
Group II	128	112	66	68
Group III	65	43	23	34
Offspring from old parents				
Group I	120	79	5	25
Group II	26	23	4	3
Group III	26	12	2	4

All the other data in table 2 included these and the rest of the females collected during the second 24-hour period. For example, 87 females produced an average of 56.6 offspring during the 0-2 day period, and 143 produced an average of 32.33 during the 2-3 day period of egg collection in the parental generation.

As shown in table 2, reproduction was initially high in all groups, gradually falling to a minimum as the age of the parents increased. The initial reproductive rate in offspring from young parents was much higher in Groups I and II than that of the parental generation, but fell below this level in Group III. The duration of the period for viable egg production was longer in offspring from young parents than in that of the parental generation, and increased in Group III to a maximum of 51 days. The number of offspring per female from middle-aged parents was lower than that of the parental generation, but values for the remainder of the reproductive period coincided fairly closely. The period of viable egg production was longer in Group I (46 days) than in the parental generation (41 days); it decreased to 41 days in II, and to 31 days in III. The initial reproductive capacity in offspring from old parents was higher than that of the parental generation, and this high rate was maintained through nine successive generations. In this group the duration of viable egg production was less than that of the parental generation (41 days). It was 36 days in Group I, 31 days in II, and 25 days in III.

Table 3 contains the average survival time of the adults in the different groups. Offspring from young parents had the same adult life span as those of the parental generation, except that females in Group I survived longer. Offspring from middle-aged and old parents had a shorter life span than those of the parental generation, except for males of Group II from middle-aged parents.

The significance of the survival values between the parental generation and offspring from young parents were calculated by dividing the difference between the means by its standard error. If this ratio ("t" value) is more than 2, the means are statistically different. Females from young parents of Group I had a significantly longer adult life than those of the parental generation, but the values for Groups II and III are not significantly different. The males and average values for females and males from young parents were not significantly different from those of the parental generation. All survival

Table 2.—Number of adult offspring obtained per female from each egg-collecting period. Group I comprises generations F_1, F_2, and F_3; Group II, F_4, F_5, and F_6; Group III, F_7, F_8 and F_9.

Egg collection period (days after emergence)	Parental generation	Young parents			Middle-aged parents			Old parents		
		Group I	Group II	Group III	Group I	Group II	Group III	Group I	Group II	Group III
0- 2	56.60	80.67	73.48	49.89	38.94	50.99	48.84	63.18	72.54	66.34
2- 3	32.33	44.79	33.31	33.23	34.08	35.99	38.96	47.52	34.97	35.40
6- 7	33.42	32.34	33.88	30.71	31.30	36.75	29.31	38.63	29.00	28.52
12-13	15.38	14.88	13.69	12.73	15.92	18.54	13.16	28.90	13.27	8.08
18-19	14.33	7.29	8.25	7.15	19.30	19.74	14.26	10.35	4.80	1.21
24-25	3.94	5.79	4.46	3.68	3.03	5.93	1.88	3.26	0.76	0.42
30-31	2.12	2.99	1.57	1.64	2.17	3.11	0.10	0.85	0.30	——
35-36	0.76	2.30	1.08	1.61	1.94	2.68	——	0.60	——	——
40-41	0.04	1.35	0.41	0.38	0.49	0.72	——	——	——	——
45-46	——	0.47	0.04	0.46	0.16	——	——	——	——	——
50-51	——	——	——	0.54	——	——	——	——	——	——

Table 3.—Average survival time (days) of the adult flies. Values are given with the standard errors. Group I comprises generations F_1 F_2 and F_3; Group II, F_4, F_5, and F_6; Group III, F_7, F_8, and F_9.

	Female	Male	Average
Parental generation			
Control	38.5 ± 1.41	40.3 ± 1.27	39.3 ± 0.96
Offspring from young parents			
Group I	42.3 ± 1.22	37.7 ± 1.62	40.4 ± 0.98
Group II	41.1 ± 1.03	36.6 ± 1.33	39.3 ± 0.81
Group III	39.9 ± 1.13	40.4 ± 1.21	40.1 ± 0.83
Average survival	41.1 ± 0.65	38.4 ± 0.80	39.9 ± 0.50
Offspring from middle-aged parents			
Group I	35.2 ± 0.84	32.0 ± 0.88	33.7 ± 0.61
Group II	34.8 ± 0.92	37.4 ± 1.06	36.0 ± 0.70
Group III	32.7 ± 1.47	32.4 ± 1.52	32.6 ± 1.06
Average survival	34.7 ± 0.57	33.5 ± 0.62	34.3 ± 0.42
Offspring from old parents			
Group I	30.9 ± 0.98	32.9 ± 1.32	31.8 ± 0.81
Group II	30.5 ± 2.17	32.2 ± 3.16	31.3 ± 1.87
Group III	30.8 ± 2.24	32.0 ± 1.97	31.2 ± 1.60
Average survival	30.8 ± 0.83	32.7 ± 1.12	31.7 ± 0.68

values for offspring from middle-aged and old parents are significantly lower than those of the parental generation with the exception of males from middle-aged parents in Group II.

The average survival times of all the adults obtained for nine generations from each parental age group are summarized in table 3. The difference between the female and male offspring and the average values for females and males from young parents and the parental generation are not significant. There is a significant lowering of the adult life span between the parental generation and offspring from middle-aged and old parents. The shortening of the adult life span in these offspring was observed in the first three generations, and there was no further decrease as the selections were maintained. Furthermore this reduction occurred in the first generation of selection. There were no consistent differences in the adult life span between offspring of different groups from parents of the same age.

DISCUSSION

The present experiments on parental age effects on adult life are in agreement with those of Ludwig (1956) and Tracey (1958) on the mealworm, *Tenebrio molitor*, and of Goetsch (1956) on *Drosophila melanogaster*. Rockstein (1957) reported that in the house fly, *Musca domestica*, only the female offspring from young parents had a greater longevity than those from old parents. The male was unaffected by this selection. However, Rockstein (1959) noted in reanalyzed data that there was a significant lowering of mortality for males derived from old females. These results were interpreted on the basis of selection of long-lived males from the longer-lived female parents still sexually functional at an advanced age. On the other hand, Comfort (1953) found no changes in the longevity of the offspring continually selected from old parents in *D. subobscura*. These selections were maintained for eight generations. In the present investigation females selected from young parents lived longer than those of the parental generation. However, only Group I showed this effect, and the results for nine generations showed no increase. Both female and male offspring from old had a shorter lifespan than those from young parents.

The observation that there were no differences in the duration of the preimaginal stages is in agreement with that of Powsner (1935), who found no effect of maternal age on the duration of the egg stage in *D. melanogaster*. On the other hand, Richards and Kolderie (1957), using the milkweed bug *Oncopeltus fasciatus* (Dall.), found that fewer eggs were laid in the very early and very late periods of reproduction. These eggs were more variable, developmental time was longer, and lower hatching percentages were obtained than from middle-aged adults. Furthermore, Ludwig and Fiore (1960), using *T. molitor*, found that an increase in parental age resulted in a decrease in the length of the larval period and in the number of larval molts. These same investigators (1961), using offspring from isolated pairs, also observed a decrease in the duration of larval but not of adult life.

Thus an increase in parental age may result in a decrease in the duration of the preimaginal stages and an increase in the rate of larval growth as in *T. molitor*, or a decrease in the rate of growth as reported for *T. obscurus* (Fiore 1960). It may result in a change in the duration of adult life as reported in the present work on *D. melanogaster*, and also by Rockstein in the house fly. There may also be a shortening in the period of viable egg production as shown in the present study.

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Studies on the Ear Mite *Otodectes cynotis*, Including Life Cycle[1]

ROBERT J. TONN

Wisconsin State College, River Falls

ABSTRACT

A survey of *Otodectes cynotis* from dogs and cats in sections of Oklahoma has been completed. The life cycle of the mite was completed on experimental hosts under natural conditions and observations were made on the life cycle stages. The epidemiology of the mite was discussed in relation to the findings of the survey and life cycle study.

Studies on the ear mite of carnivores, *Otodectes cynotis* (Hering, 1838) have, in general, been concerned with partial descriptions of life cycle stages, pathology, and treatment of the host. However, only recently Sweatman (1958) reported the life history as determined in vitro, described life cycle stages, and presented some general observations as well as a review of the literature of the mite.

This paper is concerned with a survey of *Otodectes* in cats and dogs of Oklahoma, in vivo observations on its life history and its epidemiology. The observations, in general, substantiate the work of Sweatman.

MATERIALS AND METHODS

1. Survey of the ear mite in dogs and cats in Oklahoma.

The survey of the ear mite, *Otodectes cynotis*, in dogs and cats was completed in the fall of 1956. The dogs involved were in eight kennels near Stillwater and Perkins, Oklahoma, in one in Oklahoma City, and another in the Veterinary Clinic at Oklahoma State University. The cats were farm or alley cats from approximately the same territories.

The hosts were examined by swabbing both ears with a cotton-tipped applicator; the presence of mites was determined with a hand lens or, in some cases, by examination of the ears with an otoscope.

The majority of the dogs examined were hounds; others included Terriers, Cockers, Boxers, Shepherds, Beagles, Bulldogs, Great Danes, Manchesters, Dalmatians, Dachshunds, Scotties, Greyhounds, Chows, Pekingeses, Pomeranians, Pointers, Weimaranars, and mixed breeds. The ages of the dogs ranged from 3 months to 10 years or more. The cats were all mongrels, and varied in age from kittens 5 weeks old to cats more than 4 years old. The hair coat in these cats was exceedingly diverse in length, and ranged from a short coat, like that of the Siamese, to an extremely long one, like that of the Persian.

2. Observations of *Otodectes cynotis* in vivo.

To secure data on the life cycle of the mite, experiments both under laboratory conditions, studying mites placed in containers, and under natural conditions, putting mites in the ears of noninfested kittens, were completed. In order to have suitable experimental hosts, it was necessary to examine the animals for the presence of mites by using both a swab and an otoscope. If no mites were found by these two methods, the animals were considered to be negative and suitable for experimental work. The ears of such dogs and cats after they were selected, nevertheless, were cleaned and treated with 2 percent ronnel in mineral oil or in mineral oil alone, which was a further precaution in securing mite-free potential hosts. In a week these animals were reexamined and re-treated as a further precaution and used after 2 weeks. All animals lived in isolation in cages or pens during the observations.

Transfers of the mites were made from cat to cat, cat to dog, dog to cat, and dog to dog by swabbing the ear of the host and examining the cotton-tipped applicator for mites with a hand lens before placing it in the external auditory meatus of the ex-

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perimental animal. Experience demonstrated that 20 minutes was sufficient time for the mites to transfer from the swab to the ear of the animal, and the swab was removed at the end of this period. The right ear was uniformly used for establishment of the infestations and the left ear maintained as the control. Additional animals were used in which both ears served as a control. The ears of both the experimental and control animals were examined periodically with a swab to determine infestation and migration data.

Kittens were used as hosts in studying the details of the life history of the mites. To obtain experimental infestations for life history studies a known number of mites of a stage were introduced into the right ear of each kitten. The data were accumulated by periodic inspections to determine the duration of time of the individual stages in the life history, the conditions of hatching of the eggs, and the stages of metamorphosis of the mite.

The environmental conditions under which these experiments were conducted are as follows: daily maximum temperatures ranged from 30° to 38° C. and daily minimums from 13° to 21° C., with the relative humidity varying from 50 to 90 percent.

RESULTS AND DISCUSSION

1. Survey of the ear mite in dogs and cats.

In the Stillwater and Perkins, Oklahoma areas, most of the hounds ran together occasionally on hunts, thus providing an excellent opportunity for transferring the parasites through contact. A total of 113 hounds were examined and 87 of them, or 77 percent, were infested. Considered on the basis of individual kennels, the range of incidence of infestation varied from 27 to 100 percent (table 1). This wide range was possibly due to the difference in nutritional conditions and the degree of sanitation maintained in the kennels. Those in which dogs showed the largest number of mites and the highest incidence of infestation were small and had dirt-floored pens which provided little chance for good sanitary practices. Fleas in these kennels were exceedingly abundant and probably were involved in spreading the mites from one dog to another. The dogs were given a poor diet and kept very thin, because it was the belief of the owners that the dogs would run better in this condition. The two kennels in which the dogs had the least numbers of mites were large, and were handled more efficiently by their owners. These dogs had a good diet of meat and commercial dog food, and were treated periodically to kill fleas. Although the results of the survey indicate that there was a possible correlation between the relative abundance of the ear mite and environmental factors, it was not feasible to correlate such data because the dogs were traded back and forth and conditions of the environment varied too drastically.

The kennel in Oklahoma City was managed efficiently. All of the dogs had a common area in which to feed and exercise, but each animal was given an individual sleeping area which it used. There were 134 dogs in a 7-acre pasture and 88 of them were examined; 29 dogs, or approximately 33 percent, had ear mites, but in no case was the infestation heavy. All of the dogs had been dipped periodically for flea control in a very strong mixture of crude oil and insecticides; an examination revealed that a small number of fleas was present on many of them. Several of the dogs which did not have

Table 1.—The Incidence of Infestation of Dogs and Cats with *Otodectes cynotis*.

Location of host	Number of animals examined			Number of animals infested			Percent of infestation		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
Dogs									
Stillwater Perkins Kennel									
1	9	4	13	8	3	11	89	75	85
2	9	17	26	5	12	17	56	70	65
3	5	1	6	5	1	6	100	100	100
4	13	9	22	3	3	6	23	34	27
5	6	10	16	6	9	15	100	90	94
6	6	6	12	6	6	12	100	100	100
7	8	6	14	8	6	14	100	100	100
8	7	5	12	6	4	10	86	80	83
Okla. City Kennel	40	48	88	14	15	29	35	32	33
Veterinary Clinic	11	9	20	1	1	2	9	11	10
Total	114	115	229	62	60	122	54	52	53
Cats									
Stillwater Perkins	18	18	36	4	8	12	22	44	33

ear mites had other ear infections. These conditions possibly could have had their origin in an initial infestation of ear mites or because of irritation from the strong dip used to control the fleas.

The 20 dogs examined at the Veterinary Clinic at Stillwater, Oklahoma, included those that were being used for research, as well as some patients in the clinic. Only two dogs, or 10 percent, were found to be infested with ear mites. Those two dogs, probably obtained from an animal shelter, were being used for research. The results of the survey at the Veterinary Clinic are more in accordance with other previously published reports than are those obtained in the survey of the kennel dogs. Pullar (1946) reported an incidence of 3.4 percent of ear mites from dogs in Australia, Correa (1947) in Porto Alegre, Brasil, determined that less than 3 percent of dogs in an animal shelter had mites, while Brinck (1944) in Sweden found only one infested dog in 131 that were necropsied. All of these surveys showed a much lower degree of infestation than that of the Oklahoma study, in which 50 percent of the dogs had *O. cynotis*. However, this incidence is similar to the one reported by Frost and Beresford-Jones (1958) in London, in which 44 percent of the males and 27 percent of the females examined had mites.

Thirty-six farm or alley cats were examined; 12 cats or 33 percent had ear mites. This percentage is much lower than the estimate of Stafford (1935) and Schultz (1934, 1938), who both stated that 75 percent of all cats had ear mites, and intimated that the incidence was higher in cats with long hair.

Observations in this study, as well as information supplied by veterinarians in the survey area, indicate that unilateral infestations are exceedingly rare. In fact not a single animal examined by this investigator had a unilateral infestation. Beresford-Jones (1955) reported these to be rare in dogs in London; however, Kaufmann and Frost (1949) reported 10 percent of the dogs which they examined had ear mites in only one ear.

The general condition of the ear seems to play an important role in susceptibility of ear mite infestations. The results of this study and those reported by Beresford-Jones indicate that infestations are more prevalent in dirty ears than clean ones. Dirty ears apparently may predispose them to mite infestations, or, on the other hand, their presence may be the predisposing factor to dirty ears. However, when suppuration of the ear is produced by either the ear mites or other causes, the environment of the ear is altered and the mites either die or migrate, for suppurative ears are invariably free from infestation and environment apparently is too extreme for persistence.

Sex of the host is apparently not a factor in susceptibility to the mite, even though Beresford-Jones found infestations more common in males than in females. His survey was based on dogs from an animal shelter, dogs which had the run of the streets until they were captured; it may be assumed that males would wander more extensively and have more contact than females, and thus have a greater chance to become infested. The present study was on animals confined in kennels; in these the incidence of infestation among males and females was nearly equal.

The question of the relative abundance and incidence of these mites on dogs and cats has been raised by some investigators. Beresford-Jones found that infested dogs had fewer mites than infested cats. Pullar (1946) however, in examining six dogs found two that had several hundred each. The present study was limited because none of the animals were necropsied; consequently, no accurate information concerning the number of mites could be secured. However, it appears that the number of mites on a host may be influenced greatly by environment. This opinion is based on the observation that pen-mates may show great differences in the degree of infestation, varying from heavy to light, and even absence of mites. To further substantiate the conclusion, it was determined that one male cat approximately 4 years old, even though housed with an infested male cat for more than a year, was never found to be infested. Five of six kittens of the same age which were confined in a cage for a period of a year had ear mites, while the other remained free. Furthermore, a female cat was checked periodically for over a year and was free of mites; however, her litter of three kittens became heavily infested before it was 5 weeks old. In comparing dogs and cats, it was noted that dogs were as heavily infested as cats. These observations seemed to indicate that a certain physiological or pathological condition of the ear must exist before an *Otodectes* infestation can be established. Schultz (1938) stated that the mite is quickly and easily spread from animal to animal. This may be true in many cases, but apparently the host must be susceptible to the mite before any spread, whether rapid or slow, can take place.

Many veterinarians tell their clientele that cats spread otacasiasis among dogs, and vice versa. The basis of this remark is supported by an observation of Kaufmann and Frost (1949), who wrote that probably cats are a common source of infestation of mites for the dog. In addition, Railliet and Cabiot (1892), attempted transfers from cat to cat, cat to dog, dog to cat, and ferret to dog. Their results showed that cat-to-cat and cat-to-dog transfers were possible but not always accomplished, but their dog-to-cat and ferret-to-dog transfers were entirely unsuccessful. They concluded that the mite is readily transmissible from an infested individual to negative ones of the same species, but more difficult from cat to dog and vice versa, and not possible between the ferret and dog. Sweatman (1958) however, was able to complete the in vitro life cycle of *Otodectes cynotis* in about 3 weeks on ear debris from a coyote, timber wolf, and black bear, as well as on ear debris from the usual hosts, dog, cat, and ferret. He also was able to cross breed mites from different hosts and in addition made a successful transfer of mites from a cat to a dog.

2. *In vivo* observations of *Otodectes cynotis*.

To secure more information on the interhost relation and spread of the mite and to elucidate the life history, experiments under natural conditions, putting mites in the ears of noninfested kittens, and under laboratory conditions, studying mites placed in containers, were completed. The life cycle of *O. cynotis* was determined in vitro by Sweatman (1958) to take from 18 to 28 days or approximately 3 weeks to complete. He described the life cycle stages of the mite and considered them to be the egg, larva, protonymph, deutonymph, and adult which are considered in this study.

Egg.—Immediately after oviposition, the eggs were moist, relatively soft, sticky, pearly white, oblong, subcylindrical, with one side slightly flattened, and containing an opaque mass. The egg shell soon hardened and the stickiness caused it to adhere to any substratum. Eggs were seen to adhere to mites which dragged them until the eggs dried and fell off or hatched. Eggs adhered to hairs in the ear and on the body, especially in the area between the ear and the eye. Females isolated in petri dishes deposited eggs singly, but were prone to oviposit near other eggs. When cleaning ears of hosts, it was not uncommon to obtain some pieces of cerumen with a hundred or more eggs while other pieces from the same ear contained no eggs. Hatching of isolated eggs occurred in 48 to 102 hours, with a mean of 70 hours, depending on temperature. It is doubtful whether humidity influences the time of hatching much because the shell is impermeable.

In hatching, the larva usually breaks the shell on the anteroventral surface, especially in the region of its mouthparts and legs I and II. In hatching, legs become active while the egg is still intact and when the shell breaks, the activity of the first two pairs increases to free the gnathosoma and legs I. Legs II become free soon after the first and the rest of the body follows. Occasionally the body is not completely freed immediately and the mite may carry the shell for a period of time. Mortality of mites under laboratory conditions in containers with debris is quite high because they seem to be unable to free themselves from the shell under conditions of humidities of 90 percent or more, and many are trapped in condensations of water and die.

Larva.—The small hexapod larva, averages 254 microns long and 161 microns wide in specimens from the dog, and 235 microns long and 150 microns wide in those from the cat. This is approximately the same size as the egg, and the larva grossly resembles the egg in shape, being glossy white, and semitransparent.

Larvae appeared in 4 to 7 days after females were placed in the ear of a potential host. Such larvae when removed and observed in vitro were sluggish at first, but after a few hours they became more active and moved about in the container. Legs I and II were active in locomotion while legs III were inactive and projected behind the mite. After these initial movements, a quiescent period of approximately 24 hours terminated this stage.

Protonymph.—The protonymph, the first nymphal stage, is somewhat longer than the larva and averages 306 microns long and 214 microns wide in specimens from the dog, and 278 microns long and 184 microns wide in those from the cat. The protonymph may be distinguished from the larva and deutonymph by size and the presence of a small stublike segmented leg IV, which is absent in the larva, and is present, but much smaller in the deutonymph.

Protonymphs could be recovered in 4 days after the first larvae were observed in the ears of the experimental hosts. Protonymphs were more active than the larvae and they were often found in the pinna of the ear and in the area surrounding the ear; this was not true for the larvae. Locomotion of the protonymphs is similar to that of the larvae since they use only legs I and II.

Protonymphs could be kept in containers for more than a week. After a period of activity, however, the protonymphs usually became quiescent and molted. The outline of the developing deutonymphs was never observed in protonymphs, therefore, molting apparently occurs in a very short time.

The exuviae of the protonymphs were found, but because of their transparent nature, were not observed as often as those of the deutonymph. In a study of the exuviae that were recovered, the mite appeared to have been released by an opening on the median line of the dorsum, usually toward the anterior end.

Deutonymph.—The deutonymph, the second nymphal stage, is larger than the first, averaging 391 microns long and 268 microns wide in those from the dog, and 365 microns long and 268 microns wide in those from the cat. It may be distinguished from the other stages by its size, by leg IV, which is very minute, and by the presence of a pair of adanal suckers which project from the tip of the opisthosoma.

Molting of the protonymph to the deutonymph took place in the experimental host animal in 4 to 5 days after the appearance of the first protonymphs. The deutonymph was active on emergence and the range of habitat was more extensive than that of either the larva or protonymph. It not only frequented the ear, but was found in the areas between the ear and the eye as well as other parts of the body. This and the adult stage are the most active ones, and their activity apparently accounts for the spread of the mites to potential hosts. This potential ability to spread to other animals was particularly noticeable in the experimental animals in which only one ear was infested and in which the deutonymphs and adults were the first to migrate to the control ear, where they were recovered in approximately 18 days after initial infestation with adults.

During the terminal part of this stage, the deutonymph attached itself by its adanal suckers to similar suckers of a sexually mature male and became inactive. Movement of the appendages, however, was ob-

served occasionally during the early part of this union. If they were separated manually during the earlier part of this period, the deutonymph was observed occasionally to search for another male, but if separated in the latter part of the period, it remained inactive. It was during this quiescent period that the deutonymphs developed into either males or females. In the study of the stages, it was noted that males formed unions with deutonymphs that had potential male characters. Therefore, it appears that the act is not necessarily a copulatory condition, since the deutonymph has no genital opening. However, Sweatman (1958) found that attachment with the adult male is obligatory if the ovigerous female is to oviposit, and that copulation apparently occurs at a precise moment during the molt of the female.

Adult.—The adult stage is the largest; the gravid female averages 480 microns long and 315 microns wide in those from the dog, and 447 microns long and 288 microns wide in those from the cat. It is usually larger than the male, which averages 387 microns long and 287 microns wide in the dog and 333 microns long and 248 microns wide in the cat. The female can be distinguished from other stages by size, absence of adanal suckers, presence of a short segmented leg IV, and a ventral, median, transverse genital opening; while the male can be recognized as being the size of the deutonymph, presence of adanal suckers; long, visible, segmented legs IV and a bilobed posterior end.

The sexually mature male was not observed to molt and probably does not, because the life expectancy is shorter than the female and there is no expansion of the body for sex products. The female apparently may molt after copulation. The halo appearance around some females, which could be the future exuviae, is presented as evidence. The actual molting was observed on one occasion and took place in a few seconds, the female was active immediately before and after this ecdysis.

Transfers of mites from cat to cat.—Cerumen with all stages of mites from the ear of a naturally infested male cat was placed in the right ear of a young female and two mature male cats. A month later, the ears of these three animals were examined and the female and one male had mites in both ears, but in the other male the mites were confined to the right ear. Two weeks after this examination, this unilateral infested cat was checked again and mites were found in both ears.

In another transfer, two 6-week-old kittens were used to secure information concerning the spread of mites among kittens. Twenty-five eggs were placed in the right ear of each kitten. When the ears were examined a week later, a few mites were observed in the right ears and no mites were found in the left ones; 13 days after the first examination a second one was made and eggs were present in the right ear. The infested ears contained cerumen, but the control ears showed very little cerumen and were free of mites. An examination a month later showed the control ears to contain both cerumen and mites.

Transfers of mites from cat to dog.—Two small litters of pups were used in this experiment. The first litter was composed of two long-eared, long-haired puppies about 10 to 12 weeks old, and the second one consisted to two short-eared, short-haired puppies and one long-eared, long-haired puppy about 8 weeks old. Cerumen with mites and possibly eggs was transferred from an infested cat to the right ear of each of four puppies and the fifth one was used as a control. All of the puppies were isolated individually for a month. After this interval of time, all the puppies were examined for mites. One of the short-haired pups to which a transfer had been made and the control pup had no mites, two of the long-eared, long-haired pups and the other short-eared, short-haired pup had ear mites only in the right ear. However, a month later another examination showed that both of the ears of the infested dogs had mites while the other two still remained negative.

Transfers of mites from dog to cat.—Four kittens were experimentally infested with ear mites from naturally infested dogs by using cerumen and mites on cotton swabs. These kittens died before any observations were made. The dead kittens were examined and two of them had a few mites in the ears used for the infestation, but it was not determined if these were the mites that had previously been placed in the ear or if the population had been established.

In another experiment the right ear of two kittens about 3 months old were subjected to infestation by using the cotton swab method with mites from dogs experimentally infested in a previous experiment. After these kittens were isolated individually and examined a month later, thriving populations of *O. cynotis* were present in the right ear of each kitten but no mites were found in the ears used as controls.

On the basis of these experiments and additional ones concerned with the life cycle, a total of 11 cats out of 11 became infested with mites from cats by this transfer method, 3 of 4 dogs were infested with mites from cats, and 4 of 6 cats were infested with mites from dogs. This seems to indicate that transfers between hosts of the same species are easier to accomplish than transfers between different hosts. This study further substantiates the observations of Railliet and Cabiot and those of Sweatman.

Location of Otodectes cynotis on the host.—Even though *O. cynotis* is called the ear mite, it does occur outside of the ear. All stages of the mite, particularly the deutonymphs and adults, have been observed on the skin of the head of the host, especially in the region between the ear and the eye, which is in most cats, sparsely haired. In order to determine the extent of the range of mites on the body of cats, six of them were brushed over the posterior half with a wire animal brush and the brushings were examined. This material contained many of the exuviae of nymphs and specimens of all the stages of living mites. These observations show that the mites are distributed over the body of the host. Further evidence for this and

proof that they are not confined entirely to the skin was obtained by cutting hairs from patches of skin on the flanks of kittens. These hairs were examined and exuviae, deutonymphs and adults were present. Therefore, it is shown that they are found on both the skin and the hair. Since adults, deutonymphs, and protonymphs were more numerous than larvae in all these collections, they probably are more motile. Since larvae were observed and since they are not as motile as the other stages, probably they hatched from eggs deposited there.

Generations of Otodectes cynotis in relation to epidemiology.—The potential number of generations during a period of optimum conditions for reproduction and development is important from the standpoint of epidemiology. The actual minimum time required to complete a generation is unknown and probably varies considerably, because of environmental factors, such as temperature and humidity. The approximate time necessary to complete a generation was determined by using six hosts which were experimentally infested with specific stages of the mite. Larvae usually hatched in 3 to 4 days after oviposition and lived for 1 to 4 days before molting. The protonymph stage lasted 4 to 5 days, and the deutonymph 2 to 5 days. The ages of the male and female under natural conditions could not be determined. Theoretically, the shortest life cycle based on experimental findings could be completed in less than 15 days, however, the usual time of completion varied between 18 and 25 days. The various life cycle stages could be kept for longer periods of time under laboratory conditions in petri-dish habitats than indicated by these experimental infestations. This evidence would indicate that these life cycle stages are probably even longer on the host under certain conditions.

The short duration of time to complete the life cycle shows that many mites may be produced in a very limited period and this may be related to the rapid spread. Another condition that may be related to the spread is the degree of confinement of the hosts. This was especially evident in the examination of hounds in which numerous ones were confined in small kennels, for in these the percentage of infestation was high.

Animals probably become infested in one of two ways. Evidence has been presented that the mites are capable of existing not only in the ear but on the body or off the host entirely. Consequently, the mite can easily transfer from one host to another, or from a contaminated premise to a host. In theory, at least, it is also possible for the mites to be transferred by other arthropods. Holz (1955) was successful in using house flies to transfer *Psoroptes communis* (Hering) to rabbits and *Notoedres alepis* (R. and L.) to rats. In this study stick-tight fleas, *Echidnophaga gallinacea* (Westw.), and the cat and dog fleas, *Ctenocephalides felis* (Curt.) and *C. canis* (Curt.), were capable of carrying both eggs and motile stages of the ear mite. This was determined by putting fleas in a petri dish containing all stages of the mite and observing them.

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MISCELLANEOUS PUBLICATIONS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA

Volume 2, Number 2, pp. 177-211 was issued April 13, 1961 and contains "A Revision of the North American *Cryptophagus* Herbst (Coleoptera: Cryptophagidae)" by G. E. Woodroffe and C. W. Coombs. Single copy, $2.50.

ENTOMOLOGICAL SOCIETY OF AMERICA

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The Reproductive System of *Chrysopa oculata* (Neuroptera: Chrysopidae)[1, 2]

JOSEPH C. HWANG[3] AND WILLIAM E. BICKLEY

University of Maryland, College Park

ABSTRACT

The work reported was undertaken to acquire additional information about the general structure of the Neuroptera and to provide detailed descriptions which may be used in taxonomic studies. The taxonomic value of certain genital structures of neuropteroid insects has been recognized by a number of workers, but because of the variety of terms used to designate homologous parts, a considerable amount of confusion exists. The terminology of Tjeder (1956) is accepted as the most practical for future work. Detailed descriptions and explanations of genitalic structures and comparisons with related species are given. To demonstrate its possible usefulness in taxonomy, the gonarcus, an arch-shaped structure below the anal segment, is figured along with the same structure in 8 other species.

The work reported here was undertaken to acquire additional information about the general structure of the Neuroptera and to provide detailed descriptions which may be used in taxonomic studies of the Chrysopidae. Previous investigations of the genitalia of Neuroptera have been reported by Stitz (1909a, 1909b), Newell (1918), Crampton (1918a, 1918b, 1920, 1929), Withycombe (1924), Killington and Kimmins (1932), Killington (1936, 1937), Tjeder (1931, 1938, 1954, 1956), Carpenter (1940), Ferris and Pennebaker (1939), Ferris (1940), Michener (1944), Principi (1949, 1954, 1956) and Acker (1958, 1960).

Snodgrass (1957) pointed out that apparently no studies have been made on the development of the male genital organs in the Neuroptera, and that the genitalia of the Planipennia do not resemble those of the Megaloptera and are difficult to understand.

The genitalia of several representatives of the order Neuroptera were studied by Tjeder (1954, 1956). He pointed out that many terms have been used by various authors, and he proposed a series of "neutral terms" for the genitalia which he believed would be suitable for taxonomic purposes. Tjeder's terminology with minor exceptions is here applied to the external genitalia and associated structures. The terminology for the internal structures is largely that of Snodgrass (1935) and Principi (1949).

Chrysopa oculata Say, the golden-eye lacewing, is the most common and widely distributed North American species of the family Chrysopidae (Bickley and MacLeod 1956).

Female Genitalia

(Plate 1)

External structures.—The external portion of the female genitalia (figs. 2-6) and the associated structures consist of the ectoproct (ecp), the callus cerci (cc), the ninth tergum (T 9), the anal opening (An) and the proctiger (prc), the gonapophyses laterales (gpl), the gonotreme (Gtr), the gonapophyses posterioris (gp), the praegenitale (prg) and the subgenitale (sg).

Tjeder (1956) defined the term ectoproct as follows: "lateral part of anal segment, a plate including the fused anoprocessus, cerci and catoprocessus". The anoprocessus, according to Tjeder (1954, 1956), is the uppermost process of each half of the anal segment: the cercus is considered to be the middle process which is reduced to a "callus cerci" (with trichobothria) in most Neuroptera, while the catoprocessus is the lowermost process of each half of the anal segment. Tjeder (1956) stated: "the 9th tergite forms a half-ring or is longitudinally split in its dorsal middle-line, in some Chrysopidae situated distant from the dorsum and fused with the ectoprocts on their under border, forming a kind of lateral plates". In *C. oculata* (fig. 4, ecp), the ectoproct and the ninth tergite or tergum are fused so that only a short, incomplete line of demarcation appears at the distal border between the two. The term ectoproct in *C. oculata* is equivalent to the "tenth tergite" of *C. perla* and *C. carnea* as reported by Killington (1936, 1937) and to the "tenth tergite" of *C. septempunctata* as reported by Principi (1949). However, the ninth tergite of *C. septempunctata*, which Principi (1949) named "ninth urite", is almost completely separated from the tenth tergite (ectoproct) by a distinct line of demarcation. Morse (1931) and Stitz (1931) regarded the ectoproct and the ninth tergite of *C. perla* together as the ninth tergite, but Morse (1931) added that the ninth tergite may be divided into an anterior and a posterior region. The true relationship between the ninth and tenth tergite (ectoproct) in *C. perla* was recognized by Killington (1936) when he regarded them as two structures. This author called attention to the fact that "an indistinct but unquestionable suture" separates the ninth tergite from the tenth tergite (ectoproct) just "below and cephalad to the trichobothria" in *C. perla* and *C. ventralis*. (A comparison of the line of

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[3] Present address: ADPRD, ARS, U. S. Department of Agriculture, Beltsville, Maryland.

demarcation in *C. oculata*, *C. perla* and *C. septempunctata* is given in fig. 8 a,b,c.)

The number of trichobothria in each callus cerci (figs. 2, 3, cc) varies with the individual. In three specimens of *C. oculata* examined, the number ranged from 22 to 27. In the female of *C. septempunctata*, Principi (1949) found that a few more or less than 30 trichobothria were estimated in each group.

The term proctiger was defined by Tuxen (1956) as the papilla bearing the anus. An examination of the anal opening in the female of *C. oculata* (figs. 2, 4, prc) reveals that the papilla-like, membranous structure is always associated with the anal opening and that it may project beyond the ectoproct.

Gonapophyses are defined as appendages surrounding the gonopore (Tillyard, in J. R. de la Torre-Bueno 1937). In the female they are considered by Snodgrass (1935) to be "mesal processes of the bases of the gonopods, perhaps endites, forming the first and second valvulae of the ovipositor". Tjeder (1954) used the terms gonapophyses anteriores, laterales, and posteriores. The gonophyses anteriores are associated with the eighth segment; in many Myrmeleontidae they are long, fingerlike appendages, but in various other Neuroptera they no longer exist except in the form of sternal plates. These plates, the subgenitale and the praegenitale will be discussed later. The gonopophyses laterales which are processes of the ninth tergite according to Tjeder (1954) form the sides of the ovipositor in some Neuroptera. In *C. oculata* (figs. 1-4, gpl) the gonapophyses laterales are weakly sclerotized structures, situated at the apex of the abdomen, just ventral to the anus. These structures are membranously fused dorsally, but ventrally they form a valve for the openings of the reproductive organs. The dorsal membranous connection is not seen unless the two gonapophyses laterales are pulled apart.

The colleterial gland orifice (fig. 2, CGl orifice) is observed when the gonapophyses laterales (reniformi of Principi 1949) are separated. This structure (sbocco delle glandole colleteriche) in *C. septempunctata* was figured and described by Principi (1949). She demonstrated that a small area at the dorsal surface of the colleterial gland orifice is covered densely with minute setae. These setae were not observed in *C. oculata*. Otherwise the opening is similar in both species.

Tuxen (1956) called the external opening of the common oviduct the primary gonopore, and the opening of the genital chamber the secondary gonopore or gonotreme. The term "gonopore" as used by Morse (1931) and Principi (1949), as far as can be determined, designates the opening of a genital chamber and is equivalent to the secondary gonopore or gonotreme of Tuxen (1956). This opening in *C. oculata* is here termed, gonotreme (figs. 1, 2, Gtr). It is ventrad to the colleterial gland orifice and is surrounded ventrally by a membranous, lobed structure here termed the gonapophyses posterioris (gp). Normally, the gonotreme is concealed by the gonopophyses laterales and by the gonapophyses posterioris.

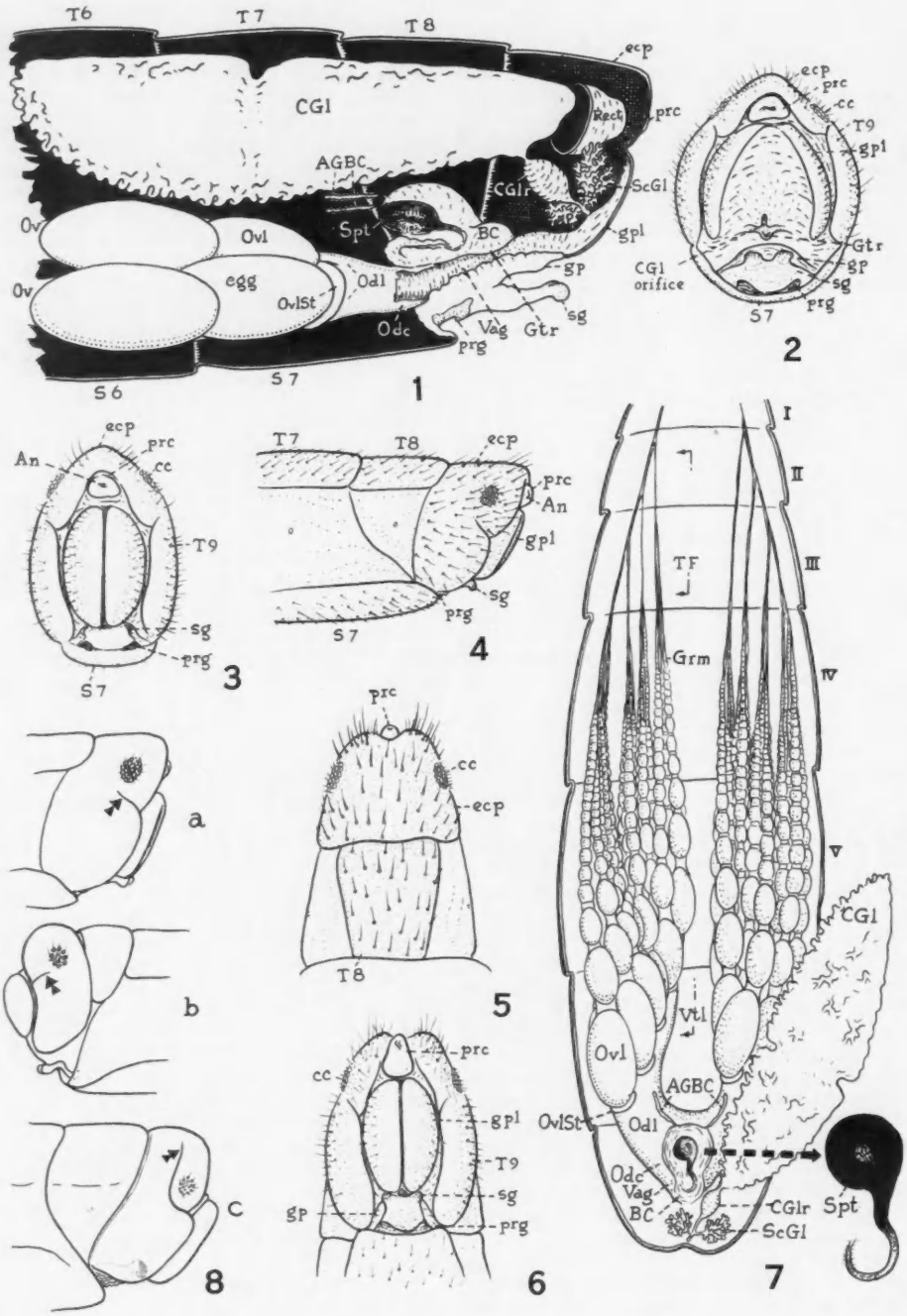
The neuropteroid gonopophyses posteriores are best developed in the Raphidiidae. *Agulla* was studied by Ferris and Pennebaker (1939) and by Ferris (1940). Tjeder (1956) indicated that the gonapophyses posteriores form the ventral part of the elongate ovipositor. In *C. oculata* the structures are unpaired and form a tonguelike membranous process above and behind the subgenitale. Occasionally the dorsal surface of this process is weakly sclerotized. This unpaired structure apparently exists in *C. septempunctata* as it was figured by Principi (1949), but that author did not name it. Its shape perhaps is variable, and its appearance depends in part on how the specimen has been preserved and in part on the angle at which it is being observed.

The subgenitale of Neuroptera according to Tuxen (1956) is the subgenital plate, covering abdominal segment VIII from below. It is equivalent to the structure which Principi (1949) referred to as the "prominenze caudali del diverticulo linguiforme", and which Killington (1936) called the eighth sternite. The subgenitale in *C. oculata* (figs. 1-4, sg) is similar to the same structure in *C. perla* and *C. septempunctata*, but is somewhat sclerotized on its dorsal surface. In addition, it is somewhat bifurcated distally. (This is also true in *Nathanica fulviceps* according to Killington 1936).

The praegenitale (figs. 1-4, 6,prg) is the unpaired plate between the apex of the seventh sternum and the subgenitale. Only the lateral angles are normally visible. Principi (1949) made no mention of such a structure, in *C. septempunctata*, but Tjeder (1954) gave a figure of the praegenitale in this insect.

Internal structures.—In general the internal structures are similar to those of *C. septempunctata* described by Principi (1949). Each ovary in *C. oculata* (figs. 1, 7, Ov) is made up of four groups or bundles of panoistic type ovarioles (Ovl). The ovarioles are divided into four parts, namely, the terminal filament (TF), the germarium (Grm), the vitellarium (Vtl) and the ovariole stalk (OvlSt). The threadlike, terminal filament of each ovariole joins anteriorly to unite several ovarioles into a group, and four such ovariole groups join and attach anteriorly to each side of the body wall. The germarium contains primordial germ cells. Vitellaria are follicles containing a series of oocytes which become gradually larger toward the oviduct. Ovariole stalks are very thin membranous tubes which serve to guide the ripened oocytes or ova into the oviduct. Based on 10 measurements from as many different individuals, the mature oocytes ranged from 0.125 mm. to 0.145 mm. in length and 0.063 mm. to 0.076 mm. in width, when the specimens are measured in physiological saline.

The lateral oviduct (Odl) serves as an opening into the common oviduct (Odc) for the passage of matured oocytes. The walls of the duct are covered by a thin circular muscle sheath. The posterior por-


T6
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Odl
OvlSt
Ov
Odc
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S6
S7
1
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T9
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CGl orifice
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2
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tion of the lateral oviduct unites with the common oviduct.

The common oviduct (Odc) is an ectodermal pouch receiving the two lateral oviducts. This pouch, located at the posterior end of the seventh segment, opens immediately into the vagina (Vag). It is difficult to differentiate between the common oviduct and the vagina. Both regions together with the bursa copulatrix constitute the genital chamber, the opening of which is the gonotreme.

The bursa copulatrix (figs. 1, 7, BC) is a flattened cavity which joins the vagina ventrally. It is assumed to be primarily a copulatory chamber and is associated with the spermatheca (Spt) but paired accessory glands of the bursa copulatrix (AGBC) are present at its anterodorsal end.

The accessory glands of the bursa copulatrix (figs. 1, 7, AGBC) are two minute, pale organs, easily confused with sections of malpighian tubules, and are attached antero-dorsally to the bursa copulatrix. Principi (1949) found these in *C. septempunctata* and called them glands of the bursa copulatrix (glandole della borsa copulatrice).

The spermatheca (fig. 7, Spt) is a dark, strongly sclerotized, spherical, coiled structure which sometimes has the appearance of a doughnut because the central part of the coil is not so dark. It is essentially a blind tube which varies in diameter. The distal portion is somewhat transparent with hair-like filaments, which were named "canalicole fecondatore" by Principi (1949).

The colleterial gland of *C. oculata* (figs. 1, 7, CGl) is in the dorsal region of the sixth, seventh, and eighth segments. It is slightly constricted transversely in the middle. Posteroventrally this gland opens into a small pouch which is here termed the colleterial gland reservoir (CGlr). Because of its location and its comparatively thick wall, it is presumed that this pouch may serve to store and regulate the outflow of adhesive substance later used to form egg stalks. At the exit of the colleterial gland reservoir, there is a common duct which joins the pouch with a pair of scent glands (ScGl), which are glandular bodies partly within the gonapophyses laterales (gpl).

Paired clusters, presently named "scent glands", (figs. 1, 7, ScGl) are seen within the gonapophyses laterales (gpl). The histology of these glands reveals: (a) that no adhesive substance is contained in the lumen; and (b) that the cellular structure of these glands shows that they are secretive in nature. Smith (1922) reported that the female *C. oculata*, when confronted by the male, began to jerk the abdomen upward and downward. In this position, it is assumed that the surfaces containing the clustered bodies may be exposed and discharge secretion as is often the case in Lepidoptera. The scent glands presently found in *C. oculata* are considered different from the similar structure in *C. septempunctata*, described by Principi (1949) as part of the colleterial glands. These glands are unrelated to the repugnatorial glands the openings of which are in the prothorax.

MALE GENITALIA

(Plate 2)

External structures.—The ectoproct (figs. 9-11, ecp), which resembles the corresponding structure in the female, is a fused structure. In the male of *Platyneuromus soror* (family Corydalidae), as illustrated by Tjeder (1954), it can be shown that the anal segment retained the three primitive processes on each hind lateral margin of the ninth tergite bordering the anus. The anoprocessus is seen at the uppermost position; the small cercus, a trichobothria-bearing structure, is situated at the middle, while the catoprocessus is seen below. A comparison of these three structures with the ectoproct in *C. oculata* shows that a fusion of these structures probably has taken place in the latter and that the cercus is reduced to a callus cerci (cc), bearing the trichobothria. The distomedian margin of the ectoproct in *C. oculata* is slightly concave. The number of trichobothria observed in each callus cerci of three male specimens varied from 18 to 21.

The proctiger in the male of *C. oculata* (fig. 11, prc), below the ectoproct, resembles the proctiger of the female. Crampton (1918b) called the proctiger the "anal tubercle".

Below the ventral margin of the ectoproct, on each side of the abdomen (figs. 10, 11, T9), is an oval-shaped sclerotized plate with the anterior end bent towards the distal area of the eighth sternum. It is believed to be the ninth tergum. Surrounding and near the dorsal border of the ninth tergum is a dark-colored groove. To the inner surface of this

FIG. 1.—Lateral view of the internal and associated structures of the reproductive organs of female *Chrysopa oculata*.

FIG. 2.—Posterior view of the external genitalia and associated structures of the female *C. oculata*. The gonapophyses laterales are extended to show other genital structures.

FIG. 3.—Posterior view of the terminal portion of the female abdomen of *C. oculata*.

FIG. 4.—Lateral view of the same.

FIG. 5.—Dorsal view of the same.

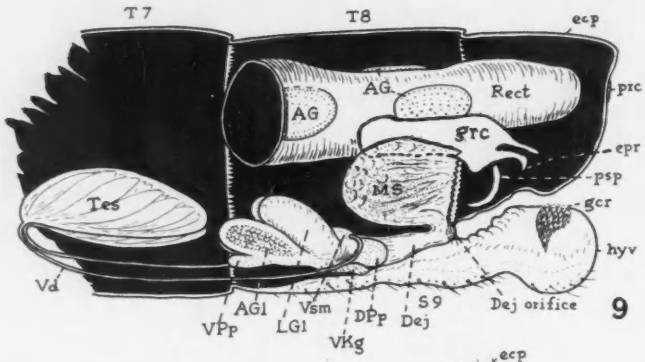
FIG. 6.—Ventral view of the same.

FIG. 7.—Ventral view of the internal reproductive system of the female *C. oculata*, with the dorsal cuticle removed. The spermatheca, much enlarged, is shown at the right.

FIG. 8.—A Comparison of the line of demarcation (pointed) between the ectoproct and the ninth tergite. (a) *C. oculata;* (b) *C. perla* (after Killington, 1936); (c) *C. septempunctata* (after Principi, 1949).

groove and the ninth tergum are attached muscles capable of projecting and retracting the gonarcus (grc), which bears the pseudopenis (psp) and a pair of membranous sacs (MS) (fig. 9).

The ninth tergite of Killington (1936) in *C. perla* is a narrow plate and is found below the ventral margin of the eighth and the tenth terga. The ninth tergite of Morse (1931) in *C. perla* appeared to be a combination of the ectoproct and the ninth tergite. Drawings of these two authors show that apparently they did not agree with each other. Crampton (1920) named a structure equivalent to the ninth tergite in



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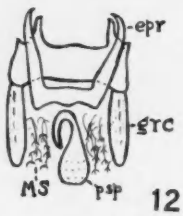

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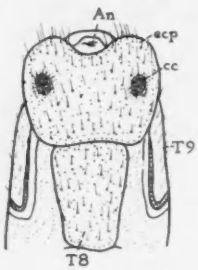

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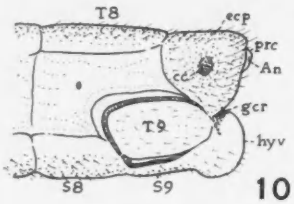

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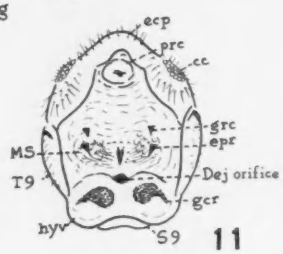

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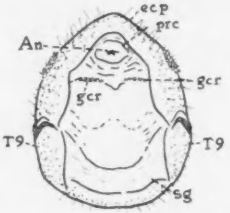

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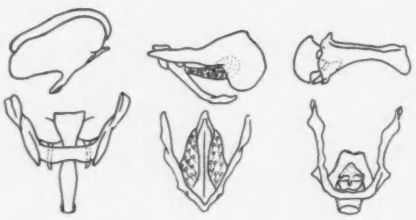

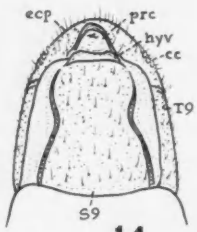

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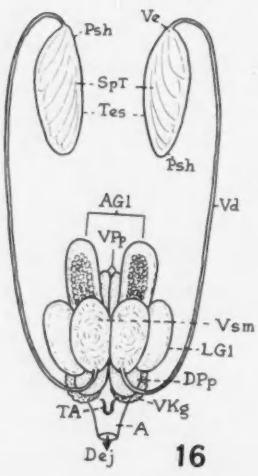

16

Nymphes myrmelionides as the "gonopleurite". Tjeder (1954) pointed out that the plate found between the ectoproct and the ninth sternite in the male *Sisyra fuscata* and *Grocus inconspicuus* is correctly known as the ninth tergite. The ninth tergum in the male of *C. oculata* resembles the corresponding structure in *C. septempunctata* and *C. flavifrons.*

The ninth sternum of the male of *C. oculata* (figs. 9, 10, S9) is a large plate and is seen ventrad to the ninth tergum. A dark incomplete groove appears at the laterodorsal margin and resembles the groove on the ninth tergum. Stitz (1931) called the ninth sternum in *C. perla* the "subgenital plate". The subgenital plate of other insects was defined by Snodgrass (1935) as the ninth abdominal sternum of the male which is extended beneath the male genital chamber, and is also known as the hypandrium. The gonapsis, which was defined by Tjeder (1954, 1956) as a structure with its apex projecting through the membrane of the ninth sternite, was not seen in *C. oculata.*

The hypovalva (hyv) is defined by Tjeder (1954) and Tuxen (1956) as the distal, unpaired produced portion of the ninth sternite. In *C. oculata* (figs. 9, 10, 11, 14, hyv) the hypovalva is the enlarged distal portion of the ninth sternum and appears as a more or less weakly sclerotized plate. On the dorsal surface of the hypovalva is a pair of sclerotized plates known as the gonocristae (gcr), which carry overlapping scalelike teeth. Each gonocrista is a retort-shaped structure with the neck pointing laterally. Gonocristae are present in many Chrysopidae, according to Tjeder (1956), and in some species they are fused into a single plate. Killington (1936, 1937) figured these plates in *C. perla* and *C. phyllochroma,* and called them "areas with scale-like teeth". In *C. septempunctata,* Principi (1949) pointed out a pair of U-shaped structures provided with microprocesses which resemble the gonocristae of *C. oculata,* and are found in the "dorsal prominence near the ejaculatory canal". Principi (1956) figures these plates in *C. clathrata.* A comparison of the left gono-

FIG. 9.—Lateral view of the internal and associated structures of the reproductive organs of the male *C. oculata.*

FIG. 10.—Lateral view of the terminal portion of the male abdomen of *C. oculata.*

FIG. 11.—Posterior view of the same. The ectoproct and the ninth sternite are extended to show the other genital structures.

FIG. 12.—Ventral view of the gonarcus, pseudopenis and the membranous sacs of *C. oculata.*

FIG. 13.—Dorsal view of the terminal portion of the male abdomen of *C. oculata.*

FIG. 14.—Ventral view of the same.

FIG. 15.—Posterior view of the same.

FIG. 16.—Dorsal view of the testes and the glandular bodies of the male reproductive system of *C. oculata.*

FIG. 17.—A comparison of the morphological variations of the gonarcus and the pseudopenis in (a) *C. perla;* (b) *C. ciliata;* (c) *C. albolineata;* (d) *C. carnea;* (e) *C. ventralis;* (f) *C. phyllocroma;* (g) *C. septempunctata;* (h) *C. clathrata* and (i) *C. oculata.* Figures a to f, inclusive, after Killington 1936, 1937. Figures g and h, after Principi 1949, 1956.

FIG. 18.—A comparison of the shape and the density of the scales on the left gonocrista of (a) *C. sensitiva* (after Tjeder 1954); (b) *C. perla* (after Killington 1936); (c) *C. septempunctata* (after Principi 1949); (d) *C. clathrata* (after Principi 1956) and (e) *C. oculata.*

LIST OF ABREVIATIONS

A	funnel-shaped ampulla
AG	anal glands
AGBC	accessory glands of bursa copulatrix
AGl	anterior glandular lobes
An	anal opening
BC	bursa copulatrix
cc	callus cerci
CGl	colleterial gland
CGlr	colleterial gland reservoir
Dej	ejaculatory duct
DPp	dorsal papilla-like protuberances
ecp	ectoproct
epr	entoprocessus
gcr	gonocristae
gp	gonapophyses posteriores
gpl	gonapophyses laterales
grc	gonarcus
Grm	germarium
Gtr	gonotreme
hyv	hypovalva
LGl	lateral glandular lobes
MS	membranous sacs
Odc	common oviduct
Odl	lateral oviducts
Ov	ovaries
Ovl	ovarioles
OvlSt	ovariole stalk
prc	proctiger
prg	praegenitale
Psh	membranous sheath
psp	pseudopenis
Rect	rectum
S	sternum
ScGl	scent glands
sg	subgenitale
Spt	spermatheca
SpT	sperm tubes
T	tergum
TA	sclerotized tongue-like structure (ampulla)
Tes	testes
TF	terminal filament
Vag	vagina
Vd	vas deferens
Ve	vas efferens
VKg	ventral kidney-shaped glands
VPp	ventral papilla-like protuberances
Vsm	seminal vesicle
Vtl	vitellarium

crista (fig. 18 a to e) or equivalent structure of Tjeder (1954) in *C. sensitiva*, of Killington (1936) in *C. perla*, of Principi (1949) in *C. septempunctata*, of Principi (1956) in *C. clathrata* and in *C. oculata* shows some obvious differences in shape and distribution of the scales. These differences may have taxonomic value.

Tjeder (1936, 1954, 1956) found the structure which he called "gonarcus" in representative males of all families of the Neuroptera but reported that it is heterogeneously developed. He stated that the gonarcus is generally situated between the anal segment and the ninth sternite, that it is an arched structure with its arches directed downward and inward, and that each arch may have a lateral process, the "entoprocessus".

In *C. oculata* the gonarcus (figs. 9, 11, 12, 17i, grc) is sclerotized and fused at the median dorsal part with the posterodorsal angles pointed posteriorly. The gonarcus is located below the rectum and appears to be held in position by two pairs of well developed muscles.

The term, gonarcus, was first used by Tjeder (1936). The gonarcus and entoprocessus were called "tenth sternite" and "parameres", respectively, by Killington (1936, 1937) and by Kimmins (1952). In the same order, they were called the wing-shaped endoskeletal projection (produzione endoscheletrica aliforme) and the hooks (uncini) by Principi (1949, 1956). The gonarcus was called "coxopodite 9" by Acker (1960).

An entirely separate, archlike structure occurs above the gonarcus in some species of chrysopids but not in *Chrysopa oculata*. Apparently the term parameres was used with reference to this structure in *Chrysopa carnea* Steph. by Killington (1937, p. 189) although he ordinarily used the term paramere to designate the entoprocessus. The structure in question was described by Principi in *C. flavifrons* Brauer and called the "transverse arch". The same structure was called "sub-rectal sclerite" by Zimmerman (1957). Adams (1959) called this structure the "gonarcus". Since the term gonarcus had been applied to another structure by Tjeder in 1936 the continuation of Tjeder's usage would prevent some confusion in the minds of subsequent workers. Principi's naming of this structure should be given consideration from the standpoint of priority, and therefore the use of the term transverse arch is advocated.

Below the gonarcus is a pair of hair-bearing membranous cavities, here termed "membranous sacs" (figs. 9, 11, 12, MS). Numerous setae are seen in each of these sacs and are directed posteriorly. Each of the setae has a tubercle at its base and is set into an alveolar cavity which has a minute opening at its base. It has been impossible to demonstrate that the alveolar cavity is associated with glandular structures by using Delafield's haematoxylin and counterstaining with eosin in 90% alcohol. However, the swelling of the setal base and the capillary opening in the cavity strongly suggests that it is secretory.

Killington (1936) found a pair of membranous sacs "attached to the tenth sternite" in male *C. perla*. He also found that a number of long setae lie together forming a projecting tuft from the opening of each sac. He suggested (1936) that these structures were possibly scent glands and later (1937) reported that "scent glands" were found in *C. ciliata*, *C. carnea*, *C. septempunctata* and *C. phyllochroma*. Principi (1949) noted such structures in *C. septempunctata* but gave no names to them.

Tjeder (1954) used the term pseudopenis to designate the tubelike unpaired organ in some Chrysopidae, and suggested that this structure was derived from the fused parameres. There are no structures resembling the more typical parameres.

The pseudopenis in *C. oculata* (figs. 2, 9, 12, 17i, psp) has a few spines at the ventral area of the base and is gradually flattened toward the apex which has membranes attached laterally. From the examination of three specimens of *C. oculata*, the pseudopenis measured approximately 0.4 mm. in length. The structure here called pseudopenis (following Tjeder) was previously called aedeagus by Tjeder (1936), by Killington (1936, 1937), and by Zimmerman (1957). It was termed the hooked process (processo uncinato) by Principi (1949) and "fused styli" by Acker (1960). The term pseudopenis is preferable.

The gonarcus (including the entoprocessus) and the pseudopenis vary considerably in shape in the various families of Neuroptera (Tjeder 1954, 1956). Variation also occurs among some *Chrysopa* species. A comparison (fig. 17 a to i) of such structures as illustrated in *C. perla*, *C. ciliata*, *C. albolineata*, *C. carnea*, *C. ventralis*, *C. phyllochroma* by Killington (1936, 1937), in *C. septempunctata*, *C. clathrata* by Principi (1949, 1956) and in *C. oculata*, indicates their potential value as taxonomic characters.

The aedeagus in some Neuroptera is known to be poorly developed and is scarcely perceptible as a distinct organ in *Corydalus cornutus*, according to Snodgrass (1957). A distinct intromittent organ is lacking in *C. oculata*. The orifice of the ejaculatory duct (figs. 9, 11, Dej orifice) is located medially in the fleshy wall of the inner part of the ninth sternum. This condition is similar to that of *C. septempunctata* as described by Principi (1949).

Internal structures.—The internal organs of reproduction of the male *C. oculata* (figs. 9, 16) consist of two testes (Tes), two vasa deferentia (Vd), and a glandular body which is made of a number of structures, and the funnel-shaped ampulla which inserts into the ejaculatory canal (Dej). The general appearance of the glandular body of *C. oculata* differs, in some respects, from that of *C. septempunctata*, as described by Principi (1949).

The testes (figs. 9, 16 tes) are situated laterally in the seventh abdominal segment, and each is covered by a membranous sheath (Psh). Within this sheath is a series of saclike testicular organs, the sperm tubes (SpT), in which spermatozoa are developed. Each sperm tube is attached at its distal

end to the vas deferens (Vd). Principi (1949) demonstrated the cellular elements and the state of development of germ cells in the sperm tube of *C. septempunctata*. The vas efferens is the narrow distal end of a sperm tube, which is attached to and opens into a vas deferens (Vd). The vas deferens arises laterally from the anterior end of each testis and extends posterolaterally to join the seminal vesicle (Vsm) at the dorsomedian surface of the latter.

The glandular body which practically surrounds the seminal vesicles consists of the lateral glandular lobes (LGl), two anterior glandular lobes (AGl), two ventral papillalike protuberances (VPp), two dorsal papillalike protuberances (DPp), the ventral kidney-shaped glands (VKg) and the funnel-shaped ampulla (A). A small, sclerotized tongue-like structure (TA) appears dorsally on the ampulla. This complex of structures is very similar to that described in *C. septempunctata* by Principi (1949). Very little is known about the functions of the various glands.

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The Reproductive System of Some Florida Mosquitoes. II. The Male Accessory Glands and Their Role[1]

PATRICK T. M. LUM[2]

Entomological Research Center, Vero Beach, Florida

ABSTRACT

In *Aedes triseriatus* Say, *A. taeniorhynchus* Wied., and *Psorophora howardii* Coq., the male accessory glands possess an anterior region whose fluid contents include large granules, and a posterior region without such granules. In the two *Aedes* species the fluid and granules are colorless, while in *P. howardii* the yellow pigmentation of the large granules makes the glandular secretion easily discernible. During mating, the fluid with its granules is always ejected along with spermatozoa and deposited with the latter in the bursa copulatrix of the female. There the granules mass compactly in the form of a rectangular or U-shaped plug, but soon begin to dissolve. In *P. howardii* the yellow pigment thus released discolors the remaining fluid in the sac, but within 24 to 36 hours the granules have completely disintegrated and no traces of the fluid are evident thereafter. There is no evidence, at present, that the fluid from the accessory glands has a stimulatory effect on the spermatozoa. The quantity of fluid in the male glands diminishes with successive matings, as does the number of spermatozoa in the seminal vesicles, and changes in the shape and appearance of the glands follow multiple matings.

Except for the studies on the male accessory glands of the silkworm *Bombyx mori* L. (Omura 1938) and the greater waxmoth *Galleria mellonella* (L.) (Khalifa 1950), there is little physiological information on the accessory glands of insects. Although the accessory glands of male mosquitoes have long been thought to play a vital role in mating, this idea has been supported almost solely by anatomical studies. The unpublished study by Burcham (1957) is the first to show evidence that the accessory glands of *Aedes aegypti* (L.) males furnish a cellular material which is ejaculated with spermatozoa during mating. Burcham also noted that the material from the glands makes up a rather large portion of the semen which is deposited in the bursa copulatrix of the female.

The specific function and the chemical nature of the fluid from the accessory glands in the male mosquito are not yet understood. Khalifa (op. cit.) observed in *Galleria mellonella* that both the fluid in the accessory glands and the spermatozoa in the seminal vesicles are depleted after one mating and that the glands required approximately 12 hours to recover, thus limiting the sexual capacity of the male. The amount of fluid in the glands was also reflected in the size of the spermatophore produced. The sexual capacity of mosquitoes is suspected to be limited only by the lack of spermatozoa (Roth 1948). Gillett (1955) also observed that *Aedes aegypti* mated without necessarily ejaculating spermatozoa but believed that seminal fluid was transferred. This present paper is concerned with the role of the accessory glands in mating and insemination of *Aedes triseriatus* Say, *Aedes taeniorhynchus* Wiedemann, and *Psorophora howardii* Coquillett.

RESULTS

In all three species the paired male accessory glands could be seen to possess an anterior region with large granules and a posterior region without large granules. In newly emerged males the accessory glands were noticeably small and undistended. Within 24 to 36 hours the accessory glands increased in size and the contents of the upper region became more granular.

The glands of all three species are capable of contracting rhythmically. As they contract the fluid contents, which are highly granular, move up and down the length of the gland, indicating the presence of a lumen extending the length of each gland.

The accessory glands of *A. triseriatus* were strikingly different from those of *A. taeniorhynchus* or *P. howardii* (Lum 1961). In the former each gland was sharply divided into two portions, the upper portion containing the large granules while the lower portion contained a fluid devoid of large particles (fig. 1).

The contents of the accessory glands are easily discernible in *P. howardii*. Unlike those of the *Aedes*, the granules in the anterior region of the glands are bright yellow in color. The glands in a newly emerged male appear transparent, with a faint tinge of yellow at the anterior ends. As the male becomes older (24 to 36 hrs.), the quantity of the fluid increases and the glands become opaque, and a brighter and bigger mass of yellow granules collects at the upper end of each gland. The transfer of this pigmented fluid to the female was thus easily followed during mating.

The fluid of the accessory glands of *A. taeniorhynchus* and *A. triseriatus* is colorless. The granular component of the fluid and the quantity also increased with age in the males of these species. In newly emerged males of *A. taeniorhynchus* and *A. triseriatus* the fluid in the glands was hardly discernible through dissection. After 24 hours or more the granular particles had increased and had become easily visible upon dissection. If the gland was punctured with a needle at the upper end, the numerous granules slowly flowed out into the surrounding medium (fig. 2).

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[2] The author expresses his gratitude to Dr. Maurice W. Provost and Dr. Jack Colvard Jones for critical reading of the manuscript.

In all species the glands of unmated 48-hour-old males were well distended with fluid, presenting a bulbous appearance. In *P. howardii* this was especially noticeable since the quantity of the fluid was reflected by the bright yellow pigmentation and opaqueness of the granules (fig. 3). Following mating, the glands underwent a striking change in shape and appearance. After two or more matings the accessory glands of *P. howardii* were no longer turgid, bulblike organs, but elongated and transparent organs devoid of bright yellow granular material (fig. 4). In glands which were not completely exhausted the remainder of the contents was seen only at the lower ends of the glands. The upper regions of the glands were first to become emptied and consequently the change was more striking at that region. The general change in shape was an elongation of the glands. Forty-eight hours after mating the changes in the glands were still prominent.

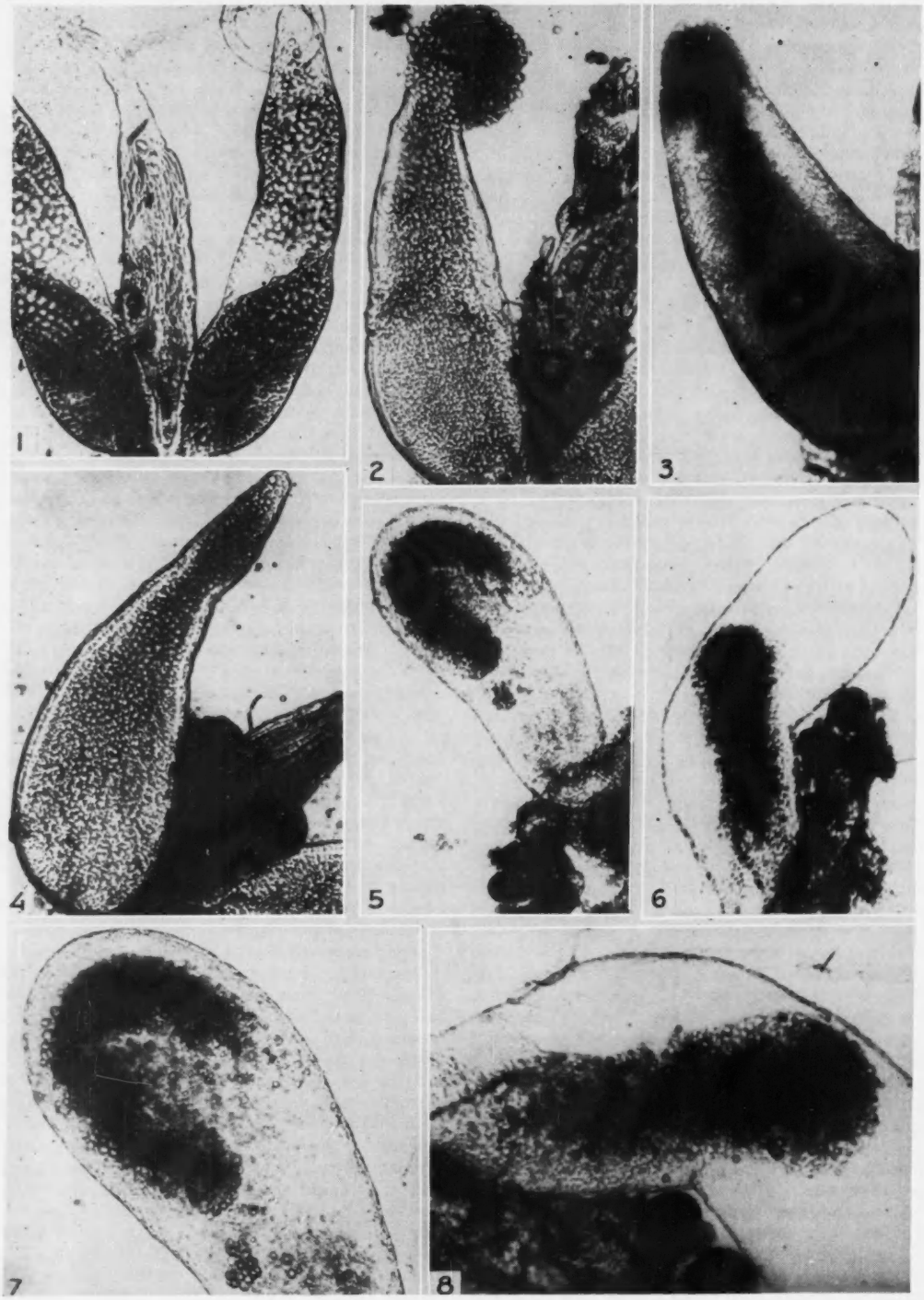
The fluid from the male accessory glands was deposited during ejaculation into a thin membranous sac or bursa copulatrix of the female. When distended after mating the bursa copulatrix was almost three times its normal size. Since the contents of the accessory glands were easily recognized in the male of *P. howardii* due to the pigmentation, a number of females of that species were examined to study the fluid as it was deposited in the bursa.

The distended bursa copulatrix in *P. howardii* was elongated and club-shaped and often in the shape of an elbow (fig. 6). The granules from the accessory glands were not dispersed freely in the bursa nor did they fill or occupy the whole interior. Instead the granules were clumped together in a very compact mass taking the shape of either a rectangular or U-shaped plug (figs. 8 and 7). The spermatozoa were dispersed throughout the sac and the mass of granules was located at either the end of the bursa or just beyond the entrance of the bursa (figs. 5 and 6). The granules alone formed only a portion of the contents in the bursa; the rest consisted of spermatozoa and the less granular fluid which contributed to the distention. The fluid furnished the medium in which the spermatozoa moved or undulated freely around the plug of granules.

The granules of the male accessory fluid apparently clustered immediately after they were released from the glands. When removed from the bursa they remained together and gradually dissolved after 2 to 3 hours. The yellow granules formed the greater part of the plug and were held together by the colorless component of the accessory fluid. Within a few minutes after mating the heavy yellow granules began to dissolve and, as a result, discolored the remaining fluid in the sac. Consequently, the entire bursa copulatrix assumed a pale yellowish color. In females which were examined 24 hours after mating the granules were almost completely dissolved and only a very slight yellowish cast was visible. Remnants of the pluglike mass of granules, then colorless, were found along with a few spermatozoa. The bursa also lost its distention and collapsed to its original form. Although spermatozoa enter the spermathecae within 15 minutes after copulation, they were still found in the bursa as long as 24 hours after mating. Since the plug of granules disappears within 24 to 36 hours, it may be similar in nature to the mating plug described by Gillies (1956) for *Anopheles gambiae*. It may also be the precursor or remnant, evolutionally, of the only dipteran spermatophore recorded, in the chironomid *Glyptotendipes paripes* Edwards (Nielsen 1959).

In order to measure the potency of a single male, multiple matings were carried out using adults of *P. howardii*. The examination of eight females which were mated singly to a 48-hour-old male showed that only the first six females were inseminated. In the first female examined 15 minutes after mating, the bursa copulatrix was well distended and a large quantity of pigmented granules was present. Two of the spermathecae contained active spermatozoa. The second female also contained a heavy quantity of pigmented granules, although the bursa copulatrix was not as fully distended as that of the first female. Spermatozoa were also present in two of the spermathecae. The bursa copulatrix was still smaller in the third, and the pigmented granules much fewer in number. The anterior tip of the bursa was not distended, showing a lack of fullness in the gland. The spermathecae were also positive for spermatozoa. In the fourth female the bursa was also nondistended and the accessory fluid was hardly pigmented, indicating that only a small quantity of pigmented granules was transferred. In the fifth and sixth inseminated females both bursa copulatrixes were nondistended and although the colorless portion of the secretion was still detectable, no trace of pigmented granules from the glands was found. Spermatozoa also were present in these females. In the male which mated with these eight females, the accessory glands were depleted of any heavily pigmented granules, although spermatozoa were still present in the upper half of the seminal vesicles. Two other groups of similar matings showed that an average of six females of nine were successively inseminated by a single male and that with each successive mating the accessory glands of the male gradually became exhausted of their contents. Complete exhaustion of spermatozoa in the seminal vesicles was never observed with males which were 48 or more hours old.

Since the quantity of fluid and granules of the accessory glands definitely diminished with each successive mating and in no case was the seminal vesicle completely devoid of spermatozoa in those which copulated without transferring sperm, indications are that the capacity of the accessory glands is also limited and that the glands are exhausted before the vesicles are. However, this remains a point of conjecture until a method is devised to measure or detect the most minute quantity of fluid present in the glands. In the series of matings conducted, sperma-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tozoa were always accompanied by some quantity of fluid from the accessory glands. Neither spermatozoa nor the material from the glands was transferred alone. The secretions from the glands undoubtedly furnish a medium for the spermatozoa during ejaculation. Since spermatozoa removed from the testes, vas deferens, or seminal vesicles are active and motile without being exposed to the fluid from the accessory glands, it is unlikely that the fluid itself has a stimulatory effect on the spermatozoa.

Results similar to those described for *P. howardii* were also obtained for *A. taeniorhynchus* and *A. triseriatus*. However, because of the colorless nature of the fluid in the accessory glands, the depletion of the fluid in the accessory glands and its presence in the female's bursa were not easily noticed in the two *Aedes*. Also, efforts were concentrated on *P. howardii* because of its mating behavior, which adapts very well to laboratory conditions. For mating experiments in the two *Aedes* species studied, the method of induced copulation (MacDaniel and Horsfall 1957) was employed.

The observations presented in this study will prove useful in our studies on the physiological state of mosquitoes and their behavior. It will be possible in field studies to collect either wild males or females and, in the case of the former, by terminalia rotation and the condition of the reproductive organs, to determine how recently mating had occurred and, in the case of the females, by the presence of the accessory fluid in the bursa copulatrix, to determine how recently insemination had taken place.

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FIG. 1.—Accessory glands of *Aedes triseriatus*, showing the anterior and posterior regions. FIG. 2.—Punctured accessory gland of *Psorophora howardii* with granules at the anterior end. FIG. 3.—Fully distended accessory gland in unmated male *P. howardii*. FIG. 4.—Accessory gland of male *P. howardii* after four matings, showing changes in shape and appearance. Granules are still present in the glands. FIG. 5.—Club-shaped bursa copulatrix of female *P. howardii*, distended after insemination. FIG. 6.—Elbow-shaped bursa copulatrix in female *P. howardii* fully distended after insemination. FIG. 7.—U-shaped plug of granules from accessory glands of male in bursa copulatrix of female *P. howardii*. FIG. 8.—Rectangular plug of granules from accessory glands of male at entrance of bursa copulatrix of female *P. howardii*.

Distribution and Repopulation of Terrestrial Insects in Sprayed Areas[1]

ELLSWORTH HASTINGS,[2] WALTER H. KITTAMS,[3] AND J. H. PEPPER[2]

ABSTRACT

Six study plots were selected to provide a variety of habitat conditions within a 132,800-acre block of forest sprayed for spruce budworm control. Changes in populations of insects were studied for 2 years following the spray application. Tests for significant differences in relative frequency of orders of insects present before spray showed a nonrandom distribution in the six sample areas. No numerical relationship could be found between the pre- and postspray populations and there was a complete lack of uniformity in the patterns of repopulation between the areas sampled. The family composition of some of the various orders of insects was found to be altered over the period of study. The most significant changes in numbers was found in the Coleoptera. No evidence was obtained to suggest any interaction between like groups in adjacent populations. They behaved differently in each sample area.

During the summer of 1955, 132,800 acres of contiguous Douglas fir forest, centering at Gardiner, Montana, were sprayed for spruce budworm control, using 1 pound of DDT in 1 gallon of No. 2 diesel fuel per acre. Of this acreage approximately 55,000 lay within Yellowstone National Park. This presented an opportunity to study the distribution and patterns of repopulation by terrestrial insects of a large, relatively undisturbed area.

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[2] Montana State College, Agricultural Experiment Station, Bozeman, Montana.

[3] National Park Service, Yellowstone Park, Wyoming; now Regional Research Biologist, Region Two Office, National Park Service, Omaha, Nebraska. The authors acknowledge the help of Dr. R. C. Froeschner with the identification of the insects.

Several studies have been made on the effects of DDT spray on terrestrial insect life. Most of these have been confined to limited areas where repopulation could be influenced by invasion from surrounding untreated areas.

Hoffman and Merkel (1948), Hoffman and Linduska (1949), and Hoffman et al. (1949) found that the invertebrate species complex can be temporarily altered, even within a relatively small treated area. However, no serious damage to the arthropod fauna was detected when 1 pound of DDT per acre was applied.

Six study sites, which afforded a variety of habitat conditions, were chosen within that portion of the control area lying in Yellowstone National Park. These plots were sampled immediately before the spray application, 15 days later, and on approximately the same dates in 1956 and 1957. All samples were obtained by taking 100 half-circle sweeps with a 15-inch-diameter insect net along each of two transects within each plot. A plot sample thus consisted of 200 sweeps. When the 1956 and 1957 samples were taken, attempts were made to duplicate as nearly as possible the time of day, general weather conditions, and transect locations.

It is recognized that samples taken in the above manner are not truly quantitative and, further, that certain groups of insects would be missed. It was felt, though, that samples taken in this manner would provide an adequate index of distribution and population changes for a majority of the insects present in the area.

RESULTS

Twelve orders of insects were represented in the collection, but only seven were sufficiently numerous to be included in an analysis of the data. These, with their population numbers, are recorded in table 1.

The data obtained in the prespray collections (July 5, 1955) were tested for significant differences in the relative frequencies of the orders present in the six sample areas. Exclusive of Collembola, which were not present in sufficient numbers to be included in the test, the results showed that the areas were not uniform as to composition ($X^2=1061$, d.f.=25, $p<.01$). This implies no numerical relationship in the distribution of the various orders within the general study area. In other words, the orders were not distributed at random. The same relationship held for the postspray collections made on July 20, 1955 ($X^2=438$, d.f.=25, $p<.01$). It was felt that with the approximately 75 percent reduction in their numbers, population pressures would differ and some redistribution of orders within the treated area might take place. This was not found to be the case.

The data were then tested to see if the different orders repopulated in proportion to the numbers originally present. The data for 1956 and 1957 were compared with those taken in the prespray collection of 1955. In all of the sampling sites except Area four, where the numbers of specimens taken were not considered adequate for statistical analysis, no numerical relationship could be found between the pre- and postspray populations. All of the X^2 values

Table 1. Numbers of specimens collected in the orders listed (1955-1957).

Area	*Hymenoptera*	*Diptera*	*Homoptera*	*Hemiptera*	*Coleoptera*	*Lepidoptera*	*Collembola*
			7-5-55 (prespray)				
1	293	342	200	138	94	42	5
2	458	727	649	444	95	192	51
3	567	438	180	187	94	243	6
4	281	359	143	111	50	76	2
5	78	100	166	152	86	68	0
6	45	55	37	222	61	37	0
			7-20-55 (postspray)				
1	57	105	123	20	6	30	106
2	142	124	148	32	10	27	28
3	272	59	123	20	27	33	5
4	51	43	38	1	11	5	1
5	47	16	85	47	15	5	0
6	16	15	25	48	10	9	0
			7-16-56				
1	438	739	681	549	55	155	2595
2	736	547	204	289	67	208	388
3	436	481	415	352	85	261	1440
4	228	267	371	318	49	17	21
5	137	185	68	280	67	19	0
6	132	243	112	86	43	101	0
			7-8-57				
1	631	1203	86	208	53	180	394
2	1043	924	120	84	126	87	40
3	553	555	119	96	56	59	1186
4	211	554	155	136	50	21	6
5	280	565	284	826	55	86	0
6	162	600	193	562	56	209	0

were significant at the $p<.01$ level. This would suggest that the original population density was not the controlling factor in subsequent repopulation behavior.

To determine if the changes in numbers for each order of insect were significant over the 3-year period an analysis of variance was made. In this analysis the data for the four sampling periods shown in table 1 were used, each order being treated separately.

While the numbers of Hymenoptera changed during the period of study, the change was not highly significant ($F=3.8$, d.f.$=23$, $p<.05$). Fourteen families and one superfamily of Hymenoptera were represented in the prespray collections, with 95 percent of the numbers being about equally distributed in the Formicidae, Braconidae, Chalcidoidea, Ichneumonidae, and Tenthredinidae. The increase in Hymenoptera during 1956 and 1957 was due to greater numbers of Chalcidoidea and Braconidae. The other 13 families did not increase appreciably in numbers over their 1955 postspray levels.

A marked increase in the numbers of Diptera took place during the 3-year period ($F=13.9$, d.f.$=23$, $p<.01$). Of the 30 families represented in the prespray collections, 69 percent of the specimens taken were in the families Chloropidae, Cecidomyiidae, Empididae, and Muscidae. The rapid upswing in numbers of Diptera in 1956 and 1957 was due almost entirely to members of the family Agromyzidae, none of the other families showing any noticeable increase in numbers over 1955 postspray collections.

The total numbers of Homoptera did not change significantly during the course of the study ($F=2.2$, d.f.$=23$, $p>.05$). There were six families represented in the prespray collections, with over 80 percent of the specimens being in the families Aphididae and Cicadellidae. The number of specimens in these two families decreased in the 1956 and 1957 collections but this decrease in numbers was offset by a corresponding increase in the numbers of Chermidae and Membracidae.

Hemiptera were represented by 11 families in the prespray collections. Of the 1254 specimens taken, 1054 or 84 percent were in the family Miridae. Although the total number of Hemiptera increased significantly during the period of study ($F=7.2$, d.f.$=23$, $p<.01$), there was no evidence to show that the increase was due to any particular family. With the exception of Nabidae and Pentatomidae, they all increased about equally, there being no indication that repopulation by mirids exceeded that of any other family. No measurable effect on the nabid population resulted from the spray. This was not the case with the pentatomids, as not a single specimen was taken during the 2-year period following the spray.

The most significant change in numbers among the insect orders studied was in the Coleoptera ($F=24.2$, d.f.$=23$, $p<.01$). Repopulation by members of this group was slow in comparison with the other orders. The prespray collections showed that over 65 percent of the individuals collected were in the families Cantharidae, Mordellidae, Elateridae, and Melyridae. This was not the case in the 1956 and 1957 collections. All of the 20 families represented appeared to make a relatively uniform but slow recovery. None of them reached its prespray population level.

The Lepidoptera population changed significantly ($F=3.8$, d.f.$=23$, $p<.05$), but no particular trend in the pattern of repopulation was evident from the data. This was likewise true for Collembola although their numbers did not change significantly ($F=2.1$, d.f.$=23$, $p>.05$).

CONCLUSIONS

The data presented in this paper lend support to the theory that most insect species are highly selective in their distribution. The data likewise lend support to the contention that each more or less isolated population behaves as an independent unit. No evidence was obtained which would suggest any interaction between like species in adjacent populations. These behaved differently in each sample area.

There was a complete lack of uniformity in the pattern of repopulation between the areas sampled. No relationship was found between prespray numbers and subsequent population growth.

No evidence was obtained which would suggest that movement from untreated areas was a factor in repopulation. This might vary somewhat, however, with the extent of the depopulated area and the migratory tendencies of the species involved.

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Repopulation by Aquatic Insects in Streams Sprayed with DDT[1]

ELLSWORTH HASTINGS,[2] WALTER H. KITTAMS,[3] AND J. H. PEPPER[2]

ABSTRACT

Population changes in Ephemerida, Trichoptera, and Plecoptera in two high-gradient mountain streams were studied over a 4-year period, following a large scale spray operation. A drastic and widespread reduction in all forms took place immediately after spraying. Trichopterans in cases of the type constructed by the family Leptoceridae were extremely numerous before spraying. No live specimens of this form were obtained during the succeeding 4-year period. Over this period, increase in numbers of Ephemerida in one stream was linear. Analysis of variance tests showed that, in every other instance, no numerical relationship existed in the repopulation of ephemerids or trichopterans. Population numbers of these two forms did not level off until 3 years after spray application. Populations of plecopterans leveled off the year following the spraying.

In early July of 1955, a 132,800-acre block of Douglas fir forest centering at Gardiner, Montana, and extending into Yellowstone National Park was sprayed by aircraft for spruce budworm control. One pound of technical DDT in 1 gallon of No. 2 diesel fuel per acre was used. No atempt was made to avoid the application of toxicant on streams draining the area. The effects of this spray application on the aquatic insect life in two streams within the treated area were studied.

The streams selected for study—namely, Hellroaring and Tower Creeks in Yellowstone National Park—differed considerably from those described by Hoffman and co-authors (1945, 1946, 1948, 1949, 1953), who conducted similar studies in Pennsylvania, West Virginia, and Maryland. These authors concluded that the effects of DDT on invertebrate forms, both aquatic and terrestrial, were transitory.

In a more recent study Graham and Scott (1959) found that DDT spray materially reduced aquatic insects immediately following the treatment. Recovery was slight during the remainder of the spray season but increased considerably during the succeeding year.

In addition to the two streams within the sprayed area a third one, Pebble Creek, was included as a check. These creeks were chosen because of the primitive, undisturbed condition of the areas drained by them. They differ slightly in size but are similar in that they are cold-water, high-gradient, rocky-bedded, silt-free mountain streams. Large portions of the Hellroaring and Tower Creek drainages were sprayed, while the Pebble Creek drainage lay outside the treated area.

Two sample areas were selected in each test stream, one being located in a riffle and the other in deeper, more tumbling water. The rocky nature of the stream beds precluded the taking of standard 1-square-foot bottom samples. The number of live specimens taken on 20 rocks, 4 to 6 inches in diameter, from each sample area was used as a measure of the population. In 1955 the streams were sampled 8 days after the spray application and again 6 weeks later. In subsequent years an additional collection was made in mid-May with the other two taken on approximately the same dates as the 1955 collections. The total numbers of specimens obtained in each year from each stream are recorded in table 1. The study was confined to three major insect groups—namely, Ephemerida, Trichoptera and Plecoptera.

The data from Pebble Creek, the check stream, show that no significant change in numbers of immature forms took place during the 4-year period of study.

RESULTS

From the data presented in table 1,B it appears as though a drastic reduction in all forms took place in Hellroaring Creek immediately following the spray treatment. This high mortality was widespread and not confined to shallow riffles, small quiet pools or the deeper or more turbulent ones. Inspection of countless rocks in each of the above situations in various sections of the creek showed the mortality to be uniform throughout the stream bed. The first postspray collection in this creek yielded 487 dead unemerged trichopterans. These forms were in tubes or cases of the type constructed by the family Lep-

Table 1.—Numbers of specimens taken for the orders listed, 1955 through 1959.

Year	Ephemerida	Trichoptera	Plecoptera
	A. Pebble Creek		
1955	328	104	88
1956	404	378	84
1957	256	240	100
1958	316	304	116
1959	874	248	66
	B. Hellroaring Creek		
1955 (postspray)	1	0	1
1956	71	7	15
1957	127	105	11
1958	245	230	23
1959	355	115	27
	C. Tower Creek		
1955 (postspray)	12	2	4
1956	440	104	61
1957	721	452	26
1958	889	876	96
1959	800	603	42

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[2] Montana State College, Agricultural Experiment Station, Bozeman, Montana.

[3] National Park Service, Yellowstone Park, Wyoming; now Regional Research Biologist, Region Two Office, National Park Service, Omaha, Nebraska.

toceridae. None of the collections taken from Hellroaring Creek throughout the succeeding 4-year period included a single live specimen of this type.

Some recovery was apparent in 1956 in both streams, although the numbers of Ephemerida and Trichoptera were considerably below the population levels reached in 1957, 1958 and 1959. For these years the increase in numbers of Ephemerida in Hellroaring Creek was linear ($F_L = 504.9$, d.f. = 1, $p < .01$). Analysis of variance tests showed that in every other instance, both in Hellroaring and Tower Creeks, no numerical relationship existed, indicating no particular design in the mode of repopulation.

A comparison of the data in table 1,A with that in table 1,A indicates that the reduction in numbers in all three orders immediately following the spray operation was also severe in Tower Creek. It was equally uniform throughout the stream bed. In subsequent years both the Ephemerida and Trichoptera increased in numbers more rapidly in Tower Creek than in Hellroaring, but in both streams there was little evidence of leveling off in populations until 1958. This does not imply, however, that the relative frequency of species was the same as in the prespray populations. Judging from the change in frequency of certain trichopteran tube types, the postspray populations apparently differed considerably in species composition from those originally present. These changes were not observed in Pebble Creek.

In both Hellroaring and Tower Creeks the plecopteran populations appeared to level off the year following the spray. Whether or not they reached their original densities cannot be determined from the data. Pebble Creek appeared to be a less productive stream than Tower, so comparisons relative to population potentials could not be made.

To what extent repopulation was influenced by invasion from the surrounding unsprayed areas could not be determined from the data. A greater proportion of the Hellroaring drainage was sprayed than was the case with Tower Creek. As a result invasion from surrounding unsprayed areas could have been accomplished more readily in Tower than in Hellroaring Creek. The data (compare table 1,B and C) suggest that invasion may have been a factor in repopulation of Tower Creek.

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Japygidae of North America, 8. Postembryonic Development of Parajapyginae and Evalljapyginae (Insecta, Diplura)[1]

LESLIE M. SMITH

University of California, Davis

ABSTRACT

The postembryonic development of *Evalljapyx facetus* L. Smith (Evalljapyginae) was found similar to that of Japyginae as reported by various authors and summarized here; in these two families the female lays a cluster of eggs hanging from a single stalk. In *Parajapyx isabellae* (Grassi) (Parajapyginae) the development differs from that in the other subfamilies, and here the female lays eggs singly, each suspended from its own stalk.

The development of the Diplura from egg to adult is properly understood by only a few entomologists in the world today, who have an interest in these primitive insects. The great majority of American entomologists are under the false impression that the first instar, as it emerges from the egg, is a small replica of the adult and differs chiefly in lacking mature sex organs. This concept is so stated in the majority of general textbooks and the subclass to which the Diplura belong is often called Ametabola, meaning without change of body form.

Our knowledge of the postembryonic development of the Diplura comes mainly from the studies of European entomologists. Grassi (1886) was probably the first to record finding an egg mass of a japygid. He described a small egg mass found in a cavity in the soil with the female in attendance. Silvestri (1905) briefly described the first instar of

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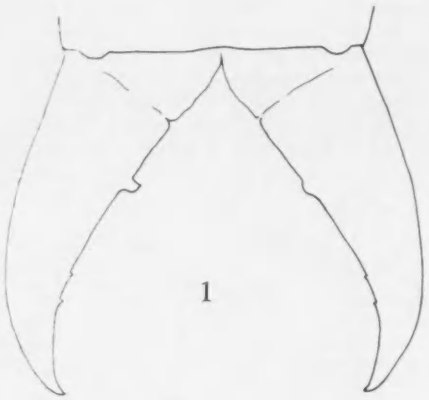
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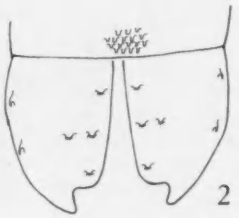
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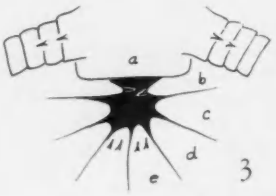
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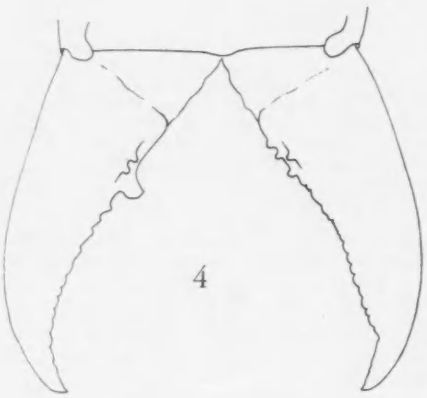
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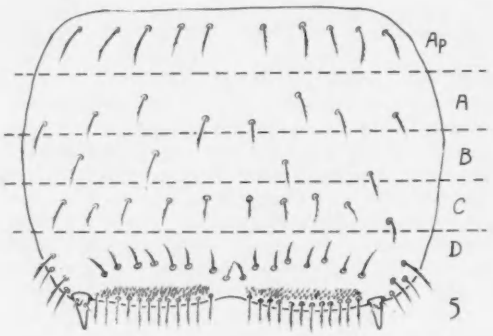
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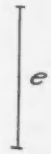
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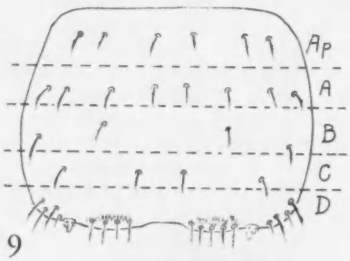
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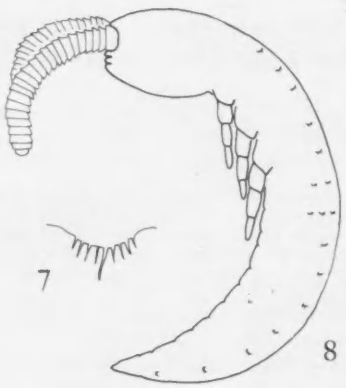
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Japyx sp. (*Japyx platensis* Silv. = *Hapljapyx platensis* (Silv.)). Later Silvestri (1928) described in considerable detail the first and second instars of *Japyx nigerianus* Silv. and noted that the first instar and early part of the second instar were spent on the egg-cluster, nonmotile, surrounded by the body of the mother. The next year Silvestri (1929) described the egg mass of *Japyx solifugus* Haliday occurring 10 to 30 centimeters deep in the soil, with 12 to 22 eggs in the mass. Parenthetically, a few years later, Silvestri (1933) described the embryonic development of *Japyx major* Grassi (=*Protjapyx maior* (Grassi)) with particular emphasis on the mouthparts. Later, Silvestri (1948) described the egg mass and the first, second, and third instars for *Protjapyx maior* (Gr.) in great detail and indicated that the first and second instars were nonmotile on the egg-cluster. More recently, the excellent studies by Von Orelli (1956) on the postembryonic development of *Campodea*, Pagés (1951) on *Dipljapyx humberti* (Gr.), and Gyger (1960) on *Dipljapyx humberti* (Grassi) have greatly increased our knowledge in this area.

All of the japygid studies thus far mentioned pertain to species in the subfamily Japyginae. Von Orelli (loc. cit) demonstrated that the male campodeid deposits spermatophores at random, and that the female (probably following the scent trail of the male) finds the spermatophore and picks it up. If we extrapolate this procedure to the Japygidae, as seems feasible in the light of present knowledge, the reproductive processes of the Japyginae can be summarized from the above authors as follows: after impregnation as postulated above, a female ready to deposit eggs, seeks an existing cavity in the soil and enlarges it by pressing movements of the abdomen, then arching the abdomen up over the thorax (Gyger 1954) secretes from the genital opening a chitinlike substance, and attaches it to the roof of the cavity to form a stalk for the hanging egg-cluster. The first-laid eggs are attached to and hang down from the stalk. Other eggs are laid attached to earlier-laid eggs to form a loose cluster resembling a bunch of grapes, or a tighter symmetrical sphere. The eggs hatch and the first instar is completely devoid of setae, nonmotile, and remains attached to the egg shell by rudimentary forceps. The second instar also occurs on the egg-cluster but possesses setae and forceps. Both instars are attended by the female. In the early part of the second instar the young japygid becomes motile and leaves the egg-cluster to lead an independent existence.

The egg laying habits and first two instars of the Evalljapyginae and Parajapyginae have not been recorded. Pagés (1952) described stages II to V for the Parajapyginae, in which stage V was considered to be adult, stages II, III and IV were considered to be nymphal, and stage I was not available. The writer has collected and studied eggs and early instars of *Evalljapyx facetus* L. Smith, and these stages are similar to those described for the Japyginae. Also, eggs and early instars of *Parajapyx isabellae* (Gr.) have been studied and these show that the egg-laying habits of the Parajapyginae differ considerably from the other two subfamilies.

The egg-cluster of *E. facetus* is similar to those described for the Japyginae. Several clusters were found in moist clay-adobe soil at a depth of 6 to 12 inches during May, at Davis, California. One egg-cluster, placed in a moist chamber but deprived of the attending female, failed to hatch. Others, attended by the female, hatched under similar conditions. The cluster is spherical and so tight that the individual eggs tend to show hexagonal surfaces. From one egg-cluster, 32 young japygids were obtained. A mother, confined in a small cage with her offspring for a few days after they became motile and left the cluster, did not attack her offspring.

The first instar of *E. facetus* (fig. 8) is immobile and remains on the egg-cluster with its rudimentary forceps fastened in the egg shell. The body is curved into a C-shape. The female (mother) stands on the cluster but is so drastically disturbed by light and dry air, that it was impossible to observe how she may attend the young. The first instar is devoid of setae but possesses a few minute spines, such as one spine at the tip of each mandibular lobe, one on each of the first two antennal segments, and two spines externally on each arm of the forceps. Segmentation of the antenna is indistinct but in older first instar nymphs, 24 segments can be counted, which is the full complement of the adult. The legs show a coxa, femur, tibia, and tarsus. The tarsus is smoothly rounded at the apex and shows no pretarsus nor tarsal claws. The mouthparts (fig. 3) consist of nine smooth lobes, which, in older first instar nymphs can be seen to contain the labrum, the mandible, the galea, the lacinia, and the labium. Thoracic and ab-

FIG. 1.—Forceps of second instar of *E. facetus* dorsal view, setae omitted e = 0.067 mm.
FIG. 2.—Forceps of first instar of *E. facetus*, ventral view. e = 0.080 mm.
FIG. 3.—Anterior view of mouthparts of *E. facetus*, first instar: a, labrum; b, mandible; c, galea of maxilla; d, lacinia of maxilla; and e, labium.
FIG. 4.—Forceps of *E. facetus* adult female, dorsal view, setae omitted e = 0.143 mm.
FIG. 5.—First abdominal sternum of *E. facetus* female, ventral view: Ap, apotome, A, B, C, D, rows of setae on sternite, e = 0.172 mm.
FIG. 6.—Egg stalk and egg shell of *P. isabellae* lateral view, e = 0.106 mm.
FIG. 7.—Setose crescent from first instar of *E. facetus*.
FIG. 8.—First instar of *E. facetus*, lateral view, e = 0.417 mm.
FIG. 9.—First abdominal sternum of second instar of *E. facetus* ventral view, labeling as in fig. 5, e = 0.110 mm.
FIG. 10.—First instars of *P. isabellae* in cavity in the soil.

dominal segments are not differentiated. Styli are absent. Subcoxal organs are absent. The forceps or cerci (fig. 2) are nonsclerotized, thick and short, and each terminates in two lobes. On their inner face are four groups of minute spines arranged in crescents (fig. 7). In the midventral posterior area of the 10th sternite is a rugose area of minute papillae.

The second instar of *E. facetus* remains immobile on the egg-cluster for about 24 hours after moulting, then leaves the cluster and begins an independent existence. It carries a full complement of adult characters (Smith 1959) except for the following: labial palpus with two long and three short setae, distal lamina of lacinia rodlike, not pectinate, lateral subcoxal organs with 5+5 sensory setae, the row of setae just anterior to the subcoxal organs and within the limits of the styli completely absent (fig. 9D), each abdominal prepleurite with a single large plumose seta, meso- and metanotal scuta with 7+7 plumose setae, abdominal tergites with plumose setae as follows: I 5+5, II 8+8, III-VIII 9+9, IX dorsal 3+3, and X dorsal 7+7. Abdominal sternites (fig. 9) apotomes with 3+3 plumose setae and sternites: I 10+10, II-V 13+13, VI and VII 14+14, VIII 6+6, IX ventral 2+2, X ventral 9+9. Left arm of forceps with a small basal tooth, right arm the same but tooth slightly smaller.

Three egg masses of *Parajapyx isabellae* (Gr.) were found during August 1944, in a clay adobe soil in a barley field near Davis, California. All were found at a depth of 2 feet. At this depth the soil was slightly moist whereas the surface 10 inches was dry. Each mass consisted of four eggs, each attached to the roof of the egg chamber by its own stalk. The eggs were laid in a straight row. The female was in attendance in each case. All of the eggs had hatched when found and the first-instar nymphs were attached by their rudimentary forceps to the inside of the egg shell. Their bodies were C-shaped and all faced in the same direction (fig. 10). The female (mother) frequently stood with her body straight inside the curved bodies of the nymphs.

The egg stalk is hollow and composed of two distinct regions. The upper part is pale amber in color, narrow at the point of attachment, widens uniformly and constricts abruptly to meet the lower portion. The lower portion is brown to dark brown, hollow, with its cavity continuous with the upper portion. Its form is ellipsoidal, slightly flattened on one side where the egg is attached. The egg is attached subapically to the lower portion of the egg stalk (fig. 6).

The first-instar nymph is similar to that of *E. facetus* except that no spines nor spiny crescents are present. In older first-instar nymphs the second instar can be seen still enclosed in the integument of the first instar. Such second-instar nymphs show the full number of antennal segments of the adult, tarsal claws, two large setae per ventral row on the tarsus, and probably the full compliment of adult body setae, but specimens available did not allow this to be completely checked, nor was it possible to study the forceps of the second-instar nymphs.

Certain measurements for *E. facetus* and *P. isabellae* are given in table I. It can be seen that the second instar was considerably larger than the first. Thus the total length increased 59 percent in *E. facetus* and 68 percent in *P. isabellae*, and other body structures increased proportionately.

Table 1.—Body measurements of *E. facetus* and *P. isabellae*, in mm.

	E. facetus			*P. isabellae*		
	First instar	Second instar	Adult female	First instar	Second instar	Adult female
Head	0.242	0.294	0.588	0.180	0.200	0.260
Antenna	0.433	0.692	1.744	0.336	0.360	0.612
Prothoracic leg	0.212	0.294	0.692	0.120	0.180	0.384
Entire animal	1.522	2.422	6.920	1.124	1.989	2.706

In both species the specimens under study had no opportunity to seek food or water, as they were immobile, attached to the egg shell. The relatively large increase in body size might be achieved by swallowing air, but newly moulted second-instar nymphs showed no air in the gut. The question therefore is unresolved whether or not the attending female supplied food or water to the immobile instars.

In the second instar the rudiments of the larger teeth appear on the forceps. They seem to be simple projections of the integument and show no relation to setae or setal origin. Consequently, japygids may be descended from those projapygids in which the cerci are armed by projections of the integument such as *Symphylurinus almeidai* Wygo., and not from projapygids in which the cerci are armed with modified setae (Smith 1960).

The absence of the setae of row D on sternite I in the second instar (*E. facetus*) and the presence of 5+5 sensory setae in the subcoxal organ suggests that these latter may be the normal body setae of row D which have migrated to the subcoxal organ and taken on a special sensory function. The normal number of body setae of row D of other sternites is 5+5. Setae appear in the row D area in later instars and increase in number with adult moults until in old males of *E. facetus* they reach 14+14. Therefore the plumose setae of row D of the first sternite in the Evalljapyginae may be of more recent evolutionary origin and may present species characters.

The quiescent first instar in the Japygidae has a counterpart in the Campodeidae (Orelli 1956) and may be considered as characteristic of the entire order Diplura. A similar first instar has been described by various authors for the classes Pauropoda, Diplopoda, Chilopoda, and for the order Collembola.

(It is absent in the Symphyla, Thysanura, and Pterygota.) The quiescent first instar in some classes has been termed the "pupoid stage" and it seems desirable to use this term also for the Diplura.

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Population Studies of the Spotted Alfalfa Aphid in Arizona in Relation to Temperature and Rainfall[1]

M. W. NIELSON AND O. L. BARNES

Entomology Research Division, Agric. Res. Serv., U.S.D.A.[2]

ABSTRACT

Following the introduction of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), in Arizona, an 87% reduction in its population occurred from 1955 to the end of 1959. Many factors were responsible. Of these, the specific effects of rainfall and temperature are discussed. Population peaks were frequent and usually occurred in April, July, and October. Rainfall was detrimental to the aphid population if a sufficient amount fell just prior to the expected buildup to initiate epizootic outbreaks of a fungus. Dates of population peaks were dependent upon temperature and relative humidity.

Populations of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), have declined steadily in Arizona since 1955. Many biotic and abiotic forces have contributed. The biotic factors have had an important effect, especially the native predators, imported parasites, and entomophthorous fungi. The abiotic factors have exercised a direct and indirect influence. The most thorough study was by Graham (1959) on the effect of humidity and temperature. All his data were taken in the laboratory where constant temperatures and humidities were maintained. Harpaz (1955), Nielson and Barnes (1957), and Padilla and Young (1958) contributed additional information, mostly gathered under field conditions.

The effect of rainfall and temperature upon field populations was the primary objective in the present study. Data on population trend, seasonal densities, and dispersion were taken during a 5-year period from 1955 through 1959. Inasmuch as a complexity of factors was involved, no effort was made to relate the effects of biotic factors except in a general sense.

Ecological Description of Area.—The study area was located in south-central Arizona in the Salt River Valley, a broad, oval, nearly flat plain about 85 miles long, 30 miles wide, and 1,100 feet above sea level. It is typically desert country with low rainfall and low relative humidity. The average rainfall during the past 65 years was 7.58 inches, with extremes from 2.82 to 19.73, both very rare, occurring only once each in 65 years. The mean temperature was 70.2° F. Daytime temperatures are frequently high during the summer months and the winters are mild. Occasional frosts occur but snowfall is very rare, although there is some on the mountains surrounding the Valley. Average daytime relative humidity, based on readings taken at 11:00 a.m. and 5:00 p.m., is 30%.

There are two rainy seasons. The first occurs from November to March, from storms that arise off the Pacific coast, although there may be periods with no precipitation for a month or so. The second

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rainy season is during July and August. These storms originate off the Gulf of Mexico and are most variable in intensity and location.

Much of the Valley is under cultivation. Approximately 500,000 acres are being irrigated from reservoirs and pumps. Alfalfa constitutes about 20% of the total irrigable acreage. In 1955, just after the introduction of the spotted alfalfa aphid, there were 103,000 acres. By the end of 1958 the acreage dropped to 85,000 owing to the high cost of production and low yields directly resulting from spotted alfalfa aphid infestations. In the spring of 1960 the acreage increased to 110,000, largely because of replacement of Chilean and African varieties by Moapa, a variety resistant to this aphid. Probably 50% of the acreage will be planted to Moapa by the end of 1960.

by Tuttle and Butler (1954). No accurate records of populations were kept during that year, but in 1955 periodic surveys were begun and continued in the Salt River Valley through 1959. Temperature and rainfall were based on records taken from three different locations.

The population trend from 1955 through 1959 is graphically illustrated in figure 1. The sharp decline during the first 3 years is striking. About an 87% reduction occurred between 1955 and 59. The decline in populations between 1955 and 56 was 50%; 1956-57, 48%; 1957-58, 24%; and 1958-59, 33%. Further decreases will probably occur as Moapa increases in the Valley. During 1959, all aphid outbreaks occurred on Chilean 21-5 and African varieties. Only very light damage was observed or reported on Moapa.

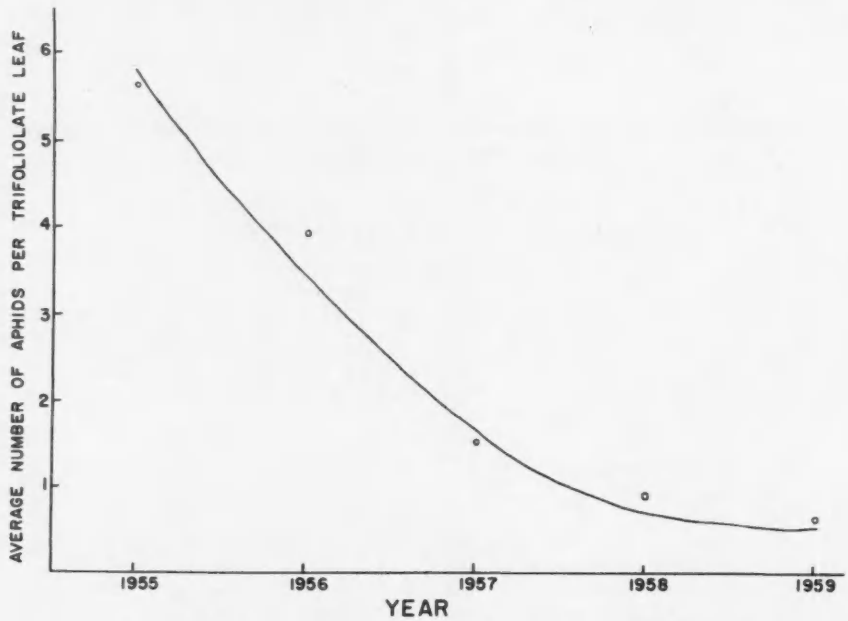

FIG. 1.—Population trend of the spotted alfalfa aphid from 1955 through 1959.

Population Trend.—Population estimates of the spotted alfalfa aphid were obtained twice monthly in 10 alfalfa fields selected at random. Aphids were counted on 30 trifoliolate leaves in each field. Details of the sampling method are given by Nielson (1957). Fields varied from 5 to 80 acres, located along a 40-mile transect running lengthwise through the Valley. Data were taken on dates of sampling, cuttings, irrigations, and insecticidal treatments. Temperature and rainfall data were obtained from climatological records furnished by the U. S. Weather Bureau, Phoenix.

In May and June of 1954 the spotted alfalfa aphid was first reported as damaging in southern Arizona

The principal factors contributing to the general decline were: Increased use of insecticides, mainly malathion, during peak densities; increased activity of predators, primarily the convergent lady beetle (*Hippodamia convergens* G.-M.); establishment of imported parasites, particularly *Trioxys utilis* Muesebeck; epizootic outbreaks of a fungus, *Entomophthora exitialis* Hall and Dunn,[3] during heavy rainfall periods; high summer temperatures; and use of Moapa.

Seasonal and Annual Fluctuations.—Population fluctuations from February 1955 through December

[3] Identified by Irvin M. Hall, Entomologist, University of California, Riverside.

1959 are illustrated in figure 2. The range shown in the upper part was based on fields having the lowest and highest average monthly population. The shaded portions illustrate the magnitude and time that they were causing serious damage in the Valley and in individual fields. Previous studies have established the economic threshold at five aphids per trifoliolate leaf. For the Valley as a whole, treatment with insecticides was required only during April and May 1955 and in June 1956. Data on populations were not available during July and August of 1956, but it was entirely possible that treatment was necessary, at least during July. As far as individual fields were concerned, there were many that needed treatment during the greater part of 1955 and 1956. Several were treated in April, July, and October, 1957; March and July 1958; and in October 1959.

Seasonal fluctuations and densities were very striking within and between years. In general, three population peaks occurred: in the spring, summer, and fall. Occasionally there was a fourth in January, but its magnitude was much less. During the 5-year period, the spring peak occurred in April except in 1958 when it took place in March. All summer peaks were in July. Fall peaks varied from September in 1956 to November in 1955, but for the most part occurred in October. Their magnitude also

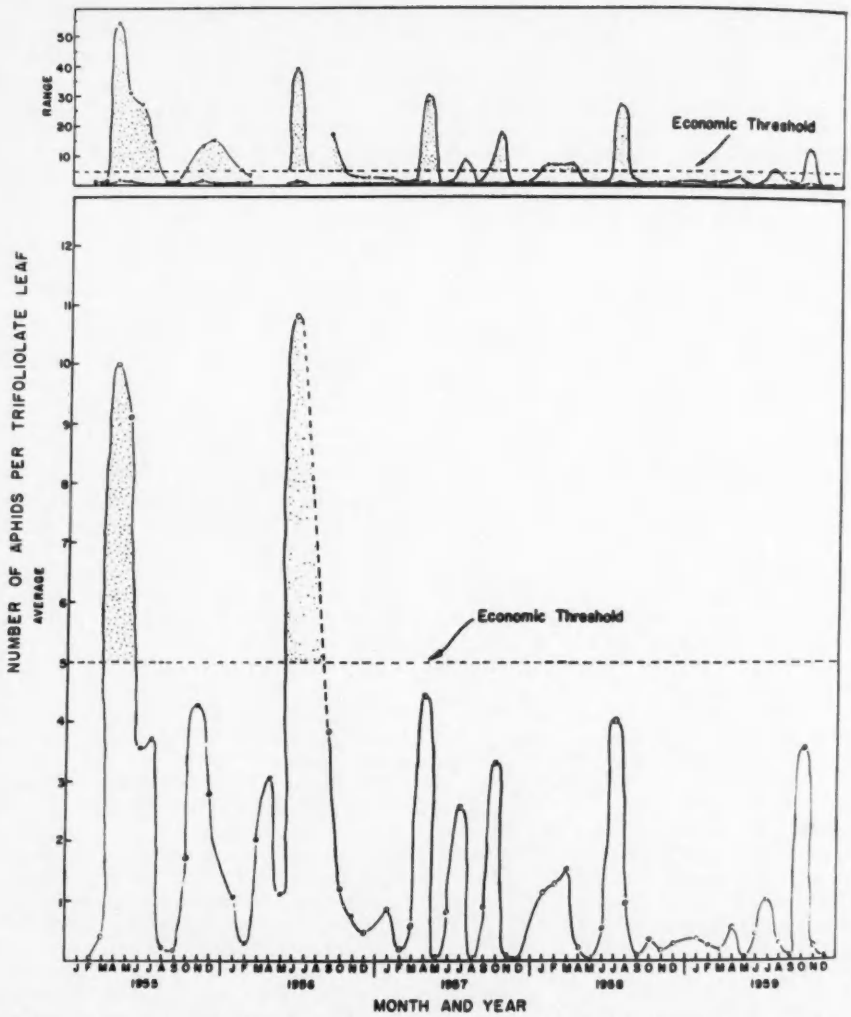

FIG. 2.—Seasonal population fluctuations of the spotted alfalfa aphid from February 1955 through December 1959.

varied from year to year. Sometimes the highest occurred in April and at other times in July or October.

In Israel, Harpaz (1955) reported three peaks in March, June, and November, and as many as 45 generations per year. Nielson and Barnes (1957) reported 35 generations a year in southern Arizona. Environmental conditions appeared similar to those in Israel. In that country the spring and summer peaks occurred 1 month earlier and the fall peak 1 month later than in the Salt River Valley. At Yuma, in southwestern Arizona where temperatures are higher, peaks were very similar to those in Israel. At Safford in southeastern Arizona the spring and summer peaks arrived 2 to 3 weeks later, and the fall peak earlier than in the Valley. In northern Arizona at elevations of from 5,000 to 7,000 feet, one aphid peak was evident, usually in July or August.

Grazing and cutting of alfalfa had some effect (Harpaz 1955). For the most part the aphids increased following grazing and subsequent rapid growth of the plants. As many as 10 grazings occurred each year. In Arizona, there appeared to be no appreciable effect from grazing or cuttings. Eight cuttings were taken in the Valley, one each in March, April, May, June, July, August, September, and November. Grazing, mainly by sheep, occurred during the winter months when populations were at a low ebb.

Dispersion and Distribution.—Several factors aid in dispersion but the least understood are those that initiate the production of winged forms. It is generally believed that overcrowding and lack of food create physiological changes in apterae and a consequent sharp increase in production of alates. Other factors such as climate and genetics possibly trigger the formation of winged aphids. Such conditions may not be applicable in this area since a sexual cycle or sequence of different forms is not consistently produced. The aphid simply produces young by parthenogenesis continuously throughout the year.

The influence of prevailing winds has not been fully determined, although they undoubtedly disseminate alates over long distances. Dickson (1959) estimated a flight of 1.4 million passing along a 1-mile front in the Colorado Desert of California. On March 10, 1956, at Yuma, Ariz., the writer observed thousands swarming out of a heavily infested alfalfa field. The day was very hot and convection currents appeared to carry them many feet into the air. On another occasion, during October 1956, swarms were observed crossing the highway near Safford, Ariz.

Methods of evaluating dispersion in southern Arizona were based on sticky-board traps similar to those originally developed by Kaloostian and Yeomans (1944). For studies of dispersion within, to, and from alfalfa fields, 10 poles were erected systematically in each of five fields selected at random in the Salt River Valley. Five traps were suspended vertically on each 2-inch x 2-inch x 6-foot pole. Each was fastened to the pole by two right-angled screws, one of which passed through a hole on top of the trap and the other below the margin to hold the trap in a horizontal position. Traps were examined for alate aphids at 2-week intervals and the number recorded. At the same time, counts were taken in fields with traps, two adjacent fields, and others in the Valley. Every month the traps were replaced.

Studies on aerial distribution and abundance of alate aphids were undertaken by selecting two water towers located about 5 miles apart in the heart of the alfalfa-growing area. One tower was 75 and the other 110 feet high. Pulleys were attached to the top of each along the catwalk. Rope of the desired length and strength was connected to the pulleys and traps were attached at 5-foot intervals to metal hooks fastened to the rope. Traps were renewed each week following examination and recording of the alates. Dispersion studies in alfalfa fields were begun in December 1955 and terminated in August 1956, and on water towers from October 1956 through August 1957.

Winged aphids found on traps from five different alfalfa fields and the populations estimated in fields with traps, those adjacent, and others are shown in table 1. Peaks of alates occurred in December 1955 and April 1956. Corresponding total population peaks were evident in other fields. Dispersion of alates was most prevalent from fields supporting peak populations. Movement was random from areas of greater to areas of lesser population. Initial infestations within fields usually started along a border; then the alates gradually spread over the entire field as continuous movement occurred. The ultimate pattern of infestation was at random. Winged aphids usually alighted on the upper portions of the plant, where they began immediate production of young. Young aphids eventually migrated to the lower parts of the plant where the environment was apparently more suitable.

Population of winged aphids collected on water towers equipped with traps and all other forms estimated in alfalfa fields are shown in table 2. Alate population peaks were evident only in April, which correspond to all forms in the field. Populations were low in July near the regions of the towers but were fairly high in other parts of the Valley. This substantiates previous findings that random distribution occurred and population densities varied from one area to another from year to year. Alate aphids were also present from 5 to 70 feet in the air with the greatest densities at 30-35 feet.

Effect of Rainfall.—Graham (1959) reported that high mortality occurred among spotted alfalfa aphids reared at 90% humidity and 95° F. and those that completed their development did not produce progeny. High humidity rarely occurred in southern Arizona except during rainfall. The direct cause of aphid mortality was a fungus, *Entomophthora exitialis*. It appeared that at least 1 inch of rainfall was required before there was any substantial aphid mortality from

Table 1.—Average populations of the spotted alfalfa aphid collected on stickyboard traps and estimated in alfalfa fields. December 1955-August 1956.

Month	Alates collected on traps						Number of alates and apterae per trifoliolate leaf		
	Field number					Number per trap	Fields[a] with traps	Adjacent fields	Other fields
	1	2	3	4	5				
December	30	4	2	1003	29	12.13	3.95	0.43	3.11
January[a]	49	1	—	3	1	0.90	0.01	0	1.40
February	1	0	0	0	1	.01	.16	0.34	0.31
March	0	5	3	18	0	.26	.39	.30	.75
April	119	8	125	244	15	6.23	.93	.21	3.35
May	0	0	19	41	0	1.50	.90	.30	1.53
June	—	—	—	—	—	—	—	—	8.89
July	0	—	—	0	0	0	0	0	—
August	0	—	—	0	0	0	0	0	—

[a] Grazing prevalent.

the fungus. Once aphids were infected, they died in a very short time. Padilla and Young (1958) reported that heavy rainfall and a fungus held populations at a low level during summer and fall in Mexico. These data suggested that high humidity or rainfall might have been directly detrimental and weakened the aphids so that they were vulnerable to a fungus attack. Moreover, rainfall apparently favored the fungus, and epizootic outbreaks resulted.

The effect of rainfall during 1955 through 1959 is shown in figure 3. Population counts were taken on dates given but rainfall as indicated represented the cumulative amount that fell from the 1st to the 15th and the 16th to the 30th days of each month.

Table 2.—Average populations of winged spotted alfalfa aphids collected on sticky-board traps mounted on two water towers, and all forms of the aphid estimated in alfalfa fields, October 1956-August 1957.

Month	Winged aphids collected on traps				All aphids in fields
	Tower 1	Tower 2	Total	Per Trap	Number per trifoliolate leaf
October	5	5	10	0.13	1.40
November	50	16	66	.68	1.42
December	19	7	26	.36	0.61
January	0	0	0	0	.64
February	0	0	0	0	.34
March	3	0	3	0.03	.63
April	112	51	163	1.77	4.48
May	53	2[a]	55	0.65	0.10
June	11	24	35	.42	.81
July	22	1[a]	23	.42	2.60
August	1	0	1	.01	0.06
Total	276	106	382	—	—

[a] Loose ropes which caused boards to rub against side of water tower gave low aphid count.

When three periods per month occurred, the rainfall data were adjusted accordingly. In 1955, heavy rains fell during the latter half of July and the first part of August. Aphid populations were increasing just prior to the rains and as a result did not reach a peak in July. Peaks were apparent in the spring and fall when little or no rain fell. Summer rainfall was so abundant and effective that the fall peak was delayed until November, the latest that it ever occurred. Approximately 62% of the total rainfall in 1955 fell during July and August. In 1956, there were only 2.73 inches, which had little effect upon peaks during that year. Precipitation in 1957 was sufficient but ineffective for aphid control except in October. The heaviest rainfalls occurred in January and October, but very little fell just prior to each population peak. Of interest, however, was the sharp decline in October. Rainfall was heavy during the second week when the population was very high. Within 1 week it was nearly wiped out. Peaks normally lasted over a period of 2 to 3 weeks before the predators, parasites, and insecticides could reduce them. Rainfall during 1958 was more effective than in any other year. Nearly 3 inches fell during February and March, which prevented a population buildup in April, the month that it usually took place. Thus, a small peak occurred in March. The most striking example of the effect of rainfall occurred when nearly 2 inches of rain fell in September, and a potential population increase was completely obliterated. In 1959, October rains almost decimated the population and were instrumental in the decline.

It is important to stress here that other factors were responsible for declines during periods of no rainfall. Insecticide use was heavy during heavy population outbreaks. Predators, mainly the convergent lady beetle, were very abundant during the spring and they effectively cleaned up aphid infestations, but not before economic loss of alfalfa had already occurred. It is also noteworthy that in spite of all the potential factors present in the field, any one

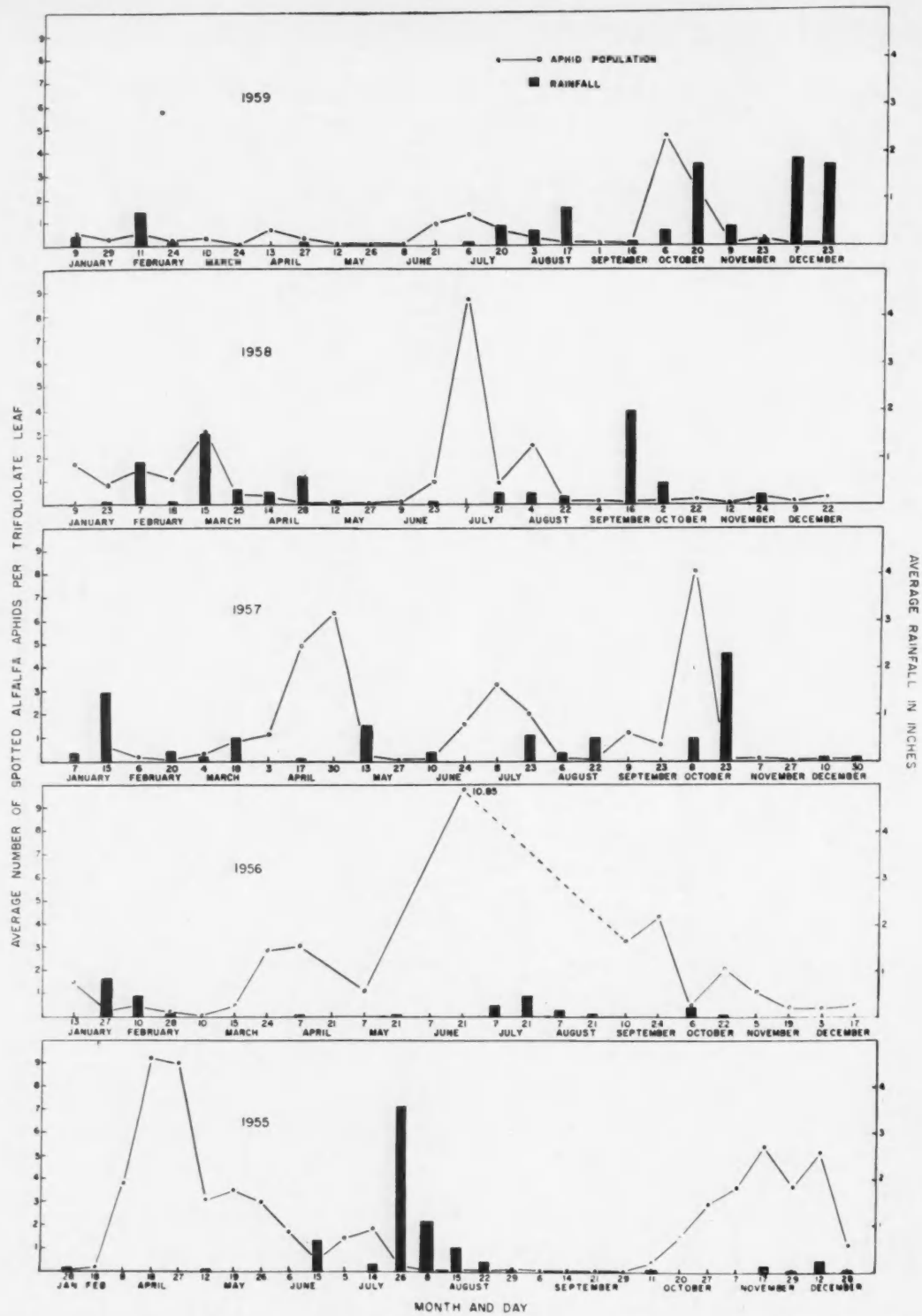

FIG. 3.—Relation of rainfall and population peaks of the spotted alfalfa aphid from February 1955 through December 1959.

of which could effectively control the aphid, population peaks still took place. Exceptions to this occurred in July 1955 and September 1958, when rainfall and subsequent epizootic attacks of a fungus effectively destroyed the aphid and prevented an outbreak.

The spotted alfalfa aphid has demonstrated a large capacity to increase in the field in a short time, a condition referred to as a "population explosion." It has been fairly easy to predict when such an event would occur. The magnitude, however, has been very difficult, if not impossible, to predict. The abiotic factors, such as rainfall, acted as a preventive, whereas the biotic factors reduced population explosions. All of these factors influenced densities, but the most important was temperature.

Temperature.—Temperature was the most important single factor affecting the biology of the aphid. Graham (1959) established threshold, minimum, maximum, and optimum temperatures for aphid development and fecundity in the laboratory. In this study it was not possible to relate temperature to the biology under field conditions, except in a general way. The data given by Graham (1959) was used as a guide to meet this end.

The relationship of mean temperature and populations over a 5-year period is shown in figure 4. Reproduction and nymphal development were apparent throughout the year although somewhat retarded during the winter months. The lowest mean temperature was 52.2° F. in January which was above the lower threshold temperature (47°) for nymphal development (Graham 1959). Reproduction was also possible in January since Graham reported 1.6 progeny per female per day at 59°. The lower threshold temperature for reproduction was not established.

The greatest population densities occurred between

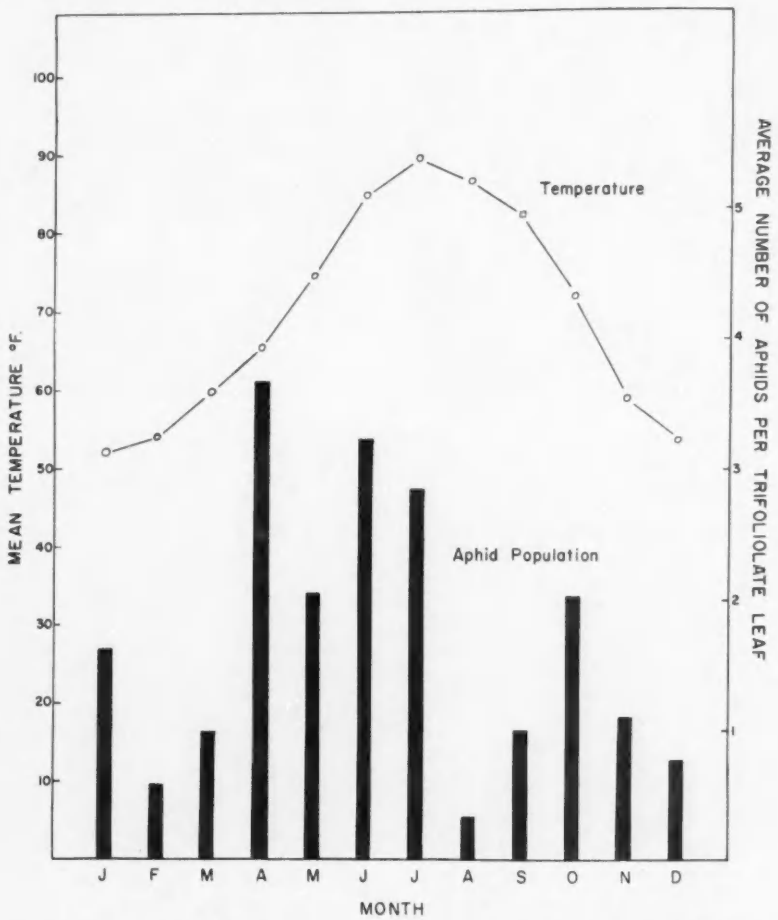

FIG. 4.—Relation of temperature and spotted alfalfa aphid populations based on 5-year average.

April and October. Mean temperatures ranged from 66.5° in April to 72.1° in October with a high of 89.2° in July. These were well below the upper threshold for nymphal development (98.6°) but were near that for maximum fecundity (77°) and optimum for nymphal development (86°) established by Graham. The maximum daytime temperatures during July and August undoubtedly had some detrimental effect. Temperatures were frequently well over 100°, sometimes reaching 115°. Thus, timing of population peaks in different areas of Arizona appeared to be because of temperature.

The data on temperature seems to be closely correlated with that of Graham. His discussion on the aphid's ability to reproduce and its rate of increase established the most favorable temperature at 86° F. with relative humidity at 25% - 30%. Such conditions are typical of southern Arizona. The high number of population peaks and the tremendous populations associated with them indicate that the warm, arid regions of Arizona are conducive to the needs of the spotted alfalfa aphid.

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Distinguishing Nulliparous from Parous Female *Culex tarsalis* by Examination of the Ovarian Tracheation[1, 2]

E. H. KARDOS[3] AND R. E. BELLAMY[4]

ABSTRACT

Techniques utilized by Russian workers for examining the tracheation of the ovaries of *Anopheles* to determine whether oviposition had occurred or not were applied to *Culex tarsalis*. Skeins or coils of tracheae were found abundantly in the ovaries of nulliparous *C. tarsalis*, but were rare in the ovaries of females that had deposited large rafts. Autogenous females depositing only small rafts had an intermediate number of knots of ovarian tracheoles. These criteria were utilized to diagnose a test series of paired ovaries from 50 females, which included approximately equal numbers of nulliparous and parous, blood-fed individuals. In this test a facility was demonstrated for distinguishing nulliparous from parous, blood-fed females, but some doubtful specimens had to be assigned to an intermediate category.

The females of most species of mosquitoes feed on blood and then mature and deposit ova. Many species are capable of more than one ovarian cycle, with each cycle generally representing a blood meal followed by maturation of eggs. After deposition of eggs a female mosquito tends to resume its original appearance. Therefore, it is difficult, if not impossible, to determine by superficial examination whether a female has oviposited. To solve this problem, students of the age structure of mosquito populations have resorted to the study of internal changes that result from oviposition.

Mer (1932) found that the ampullae of the oviducts of *Anopheles saccharovi* were small in recently emerged females but were larger in specimens that had oviposited. In studying populations of *Anopheles gambiae*, Gillies (1954) used the size of the ampullae and other internal characteristics as aids in the differentiation of nulliparous females (those that had never deposited ova) from "multiparous" females (those that had deposited at least one clutch of eggs).

More precise tools for determining the previous ovarian activity of female *Anopheles* were discovered by Russian investigators (Detinova 1945; Polovodova 1947, 1949). These and other Russian studies on this subject were reviewed by Gillies (1958) and by Detinova (1959). "Polovodova's method" was based on the finding that each time an egg was shed from an ovariole, a scar or so-called "corpus luteum" was formed; the largest number of these on any ovariole thus indicated the number of clutches of eggs deposited. Detinova (1945) observed that in the ovaries of nulliparous *Anopheles* the tracheoles were coiled in knots at the ends of the tracheae, but

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[3] Bureau of Vector Control, California State Department of Public Health, P. O. Box 1564, Bakersfield, California.

[4] Technology Branch, Communicable Disease Center, Bureau of State Services, Public Health Service, U. S. Department of Health, Education, and Welfare, P. O. Box 1564, Bakersfield, California.

that once eggs were developed the tracheoles were irreversibly stretched so that the knots were no longer present. The present study is a preliminary evaluation of the application of the latter technique to *Culex tarsalis*.

MATERIALS AND METHODS

The material examined was all from the Bakersfield colony of *C. tarsalis* in which autogeny occurs (Bellamy and Kardos 1958). Ovaries of several hundred specimens were dissected and examined. Included in the study series were more than 100 specimens in each of the following three categories:

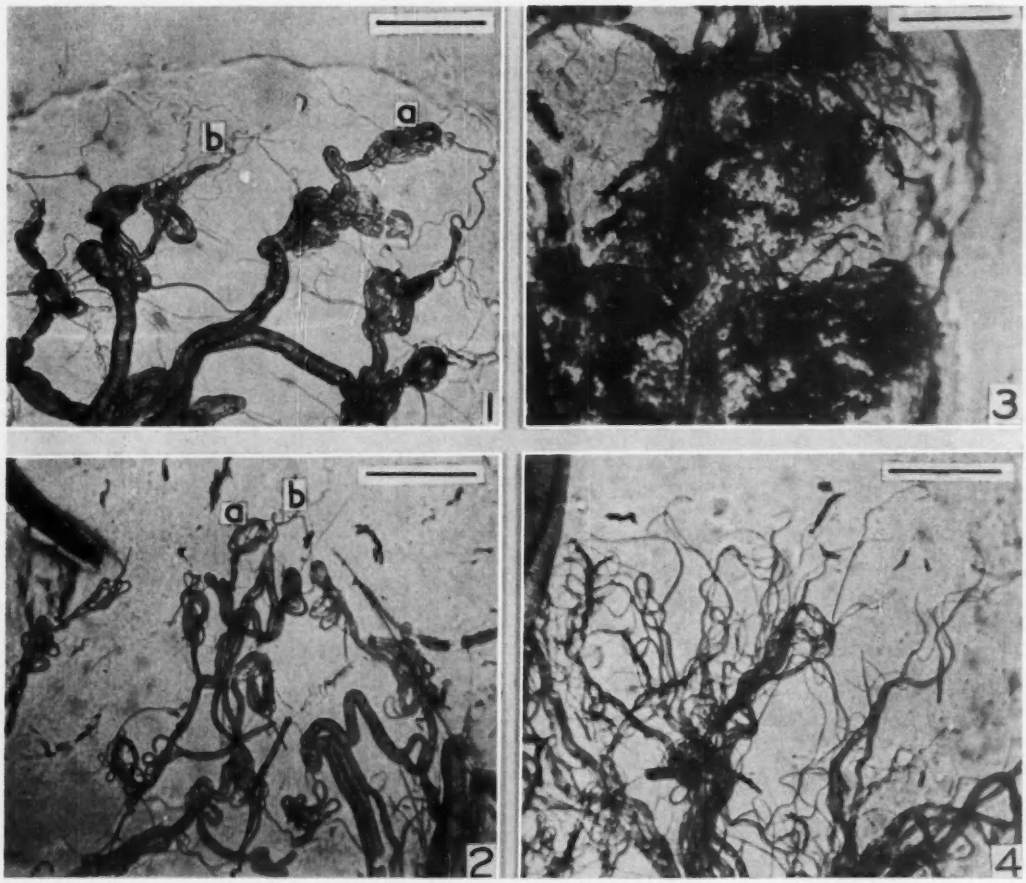
(1) nulliparous—females that had not laid eggs; none of the nulliparous females used had mature ovaries and none were blood-fed

(2) parous-blood-fed—females that had matured and deposited eggs following a blood meal

(3) parous-autogenous—females which although not fed blood deposited eggs

Among the parous-blood-fed individuals, a few took only a small quantity of blood; but most fed to repletion. Also included in the study series were 14 females held alive in outdoor cages for 3 or more months during late winter and spring before being dissected and examined. Nine of these were nulliparous, four were parous-blood-fed, and one was parous-autogenous.

Detinova's (1945) techniques were followed with a little modification. Each specimen was dissected in a drop of distilled water on a glass microscope slide under 10X magnification. The anterior part of the abdomen was gripped with one pair of forceps while with a second pair the seventh abdominal segment was clasped and slowly pulled posteriorly. This procedure ruptured the abdomen and exposed the



Photomicrographs of portions of the ovaries of *Culex tarsalis*. Scale line in each photomicrograph is 50μ.

FIG. 1.—Nulliparous ovary, a. tightly coiled skein, b. terminal filaments.

FIG. 2.—Nulliparous ovary, a. looped skein, b. terminal filaments.

FIG. 3.—Dark cloudy formations obscuring skeins and terminal filaments.

FIG. 4.—Parous ovary with open skeins.

ovaries, gut, and Malpighian tubules. The ovaries were removed, transferred to a clean, dry microscope slide, and allowed to dry. Sometimes in arranging the ovaries on a slide, they were stretched slightly, so that they would dry flattened and extended. The ovaries were examined under 400X magnification immediately after drying or up to several months later.

RESULTS

In nulliparous females, the ovarian tracheoles were arranged at the ends of the tracheae in coiled skeins or nodules, which were tightly knotted (fig. 1,a) in some cases or more loosely looped (fig. 2,a) in others. Only an occasional skein appeared uncoiled. There were a few terminal filaments extending from each skein (fig. 1,b and fig. 2,b). In most preparations of the ovaries of nulliparous females, dark, clouded areas developed soon after drying (fig. 3) and tended to obscure the skeins. Clouding was less frequent in the ovaries of parous females.

In the ovaries of parous-blood-fed females that had deposited a normal raft (usually 200 or more eggs), almost all skeins were uncoiled resulting in a network of tracheolar filaments (fig. 4). In 16 parous-blood-fed females, the number of coiled skeins remaining per pair of ovaries averaged five (range 0 to 10). The number of skeins persisting after deposition of a second egg raft was not determined. In general, the ovaries of specimens that had deposited small rafts contained fewer skeins than the ovaries of nulliparous females. However, they contained more than the ovaries of females that had deposited larger rafts. This intermediate condition was typical of parous-autogenous females and was found in some parous-blood-fed females that had taken only a small blood meal.

The four parous-blood-fed females that were held alive three or more months in outdoor cages had typical ovaries for the parous-blood-fed group (i.e., there was no reversal to coiled nodules). In nulliparous females held for similar periods, the skeins remained.

EVALUATION OF THE TECHNIQUE

These preliminary studies indicated that the condition of ovarian tracheation offered a promising tool for distinguishing female *C. tarsalis* that had oviposited from those that had not. To test the efficacy of the technique with "unknown" material, one of us (R.E.B.) prepared a test series of 50 specimens by the method described. Each pair of dissected ovaries was placed on a separate numbered microscope slide, and its history was recorded on a "key list." Twenty-four nulliparous and twenty-two parous-blood-fed females were used, and four parous-autogenous females filled out the series. The parous-autogenous specimens were included to make the test more difficult. The ovaries of specimens that had deposited only small egg rafts were known to be difficult to interpret. The numerical arrangement of the 50 slides of three different categories of ovaries was randomized.

The 50 preparations were examined and diagnosed by E.H.K., who knew only that the test series consisted of approximately equal numbers of nulliparous and parous-blood-fed individuals and that a small number of parous-autogenous individuals were included. The examination and diagnosis of the 50 slides required less than 2 hours. Since the typical ovarian tracheation of parous-autogenous individuals is intermediate between that of nulliparous and parous-blood-fed females, all intermediate and doubtful specimens in the test series were placed in the parous-autogenous category. Accordingly, this category was used for assignment of all specimens that could not be assigned with confidence to either extreme condition. Results from this test compared to the key list were as follows:

23 specimens were diagnosed as nulliparous
(22 were correctly diagnosed and one was parous-autogenous)
17 specimens were diagnosed as parous-blood-fed
(16 were correctly diagnosed and one was parous-autogenous)
10 specimens were assigned to the catch-all category, parous autogenous
(2 were parous-autogenous, 6 were parous-blood-fed, and 2 were nulliparous)

Note that none of the nulliparous specimens were diagnosed as parous-blood-fed, nor were any parous-blood-fed specimens interpreted as nulliparous.

DISCUSSION

Egg development and oviposition by *C. tarsalis* result in changes in the ovarian tracheation. These changes parallel closely the changes Detinova (1945) reported in the ovaries of *Anopheles*. The uncoiling and stretching of the tight knots of tracheoles in the ovaries of *C. tarsalis* has a direct relation to maturation of ova and only an indirect relation to blood-feeding. If a blood meal was a prerequisite to egg development by *C. tarsalis*, the condition of the ovarian tracheation would indicate quite reliably whether or not a blood meal had been taken. This is supported by the record from diagnosing a test series of specimens. The intermediate conditions in ovarian tracheation that result when only a small number of ova are matured and deposited are difficult to interpret. Females that have taken no blood but develop eggs autogenously characteristically possess such intermediate conditions. The reason for this is that they usually develop and deposit less than 125 eggs as compared to the more than 200 usually developed by females that have taken a full blood meal. Females with an interrupted blood feeding also may develop only a small number of eggs, and the range in the number of eggs they produce overlaps the number from autogenous females. Therefore, when ovarian tracheation is intermediate, to attempt an exact diagnosis of history is unwise. In-

stead, it is best to interpret that such a specimen "*probably* deposited a smaller than average egg raft, perhaps autogenously." If such ovaries are always recognized and are assigned to an intermediate "middle" group, the errors made in assigning all other specimens to the two extreme categories, "nulliparous" and "parous-blood-fed", should be minimized. This was the case in the diagnosis of the test series.

The dark clouded areas that develop in the preparations of ovaries of most of the recently emerged nulliparous females tended to obscure the tracheation but were not diagnostic of the nulliparous condition, because the same condition was seen occasionally in the ovaries of parous specimens. In subsequent studies (Burdick and Kardos, unpublished), it was found that re-wetting such preparations with a drop of water dispelled the clouding.

In studies of the natural history of mosquito-borne encephalitis viruses, there has been a great need for techniques that would permit differentiation of mosquitoes that had not taken blood and therefore could not be infected from those that had taken at least one blood meal and so might be infected. Application of such techniques to studies of overwintering or hibernating mosquito populations should provide some answer to the question, "Does the overwintering population of adult female *C. tarsalis* include individuals that have taken a blood meal?" The techniques and criteria described above, if applied with caution, should provide reliable data to answer these questions.

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Two New Species of *Neodiprion* from Southeastern North America (Hymenoptera: Diprionidae)[1]

HERBERT H. ROSS

Illinois Natural History Survey, Urbana

ABSTRACT

Neodiprion **warreni,** reared from *Pinus echinata* in Arkansas, and *N.* **merkeli,** from *Pinus eliottii* var. *densa* in Florida, are described and illustrated. The characters of *N. merkeli* suggest that it might be either a primitive member representing a form ancestral to the specialized *pini-rigidae* complex, or a species of hybrid origin resulting from a cross between a member of that complex and one of the *virginianus* complex.

The two new species described in this paper belong to the *Neodiprion virginianus* complex. In the several species already described within the complex, the teeth of the saw are large, as previously illustrated (Ross 1955, fig. 3), whereas in the new species described in this paper the saw teeth are numerous and unusually small, at least on annuli 2, 3, and 4.

It is with great pleasure that I express my appreciation to Dr. Lloyd Warren, University of Arkansas, and to Mr. O. G. Langdon and Mr. E. P. Merkel, U. S. Forest Service, who reared the species and made them available for study.

[1] Accepted for publication November 19, 1960.

Neodiprion warreni n. sp.

FEMALE.—Length from tip of head to apex of abdomen, 8.5 mm. Color chiefly brown with blackish suffusions; head orange brown with eyes, antennae, and irregular areas around the ocelli and bases of antennae black; thorax slightly paler brown, with pronotum, posterior V of praescutum, and scutellum straw color, other dorsal areas of thorax suffused with a darker shade; abdomen with dorsum suffused with blackish areas, lateral areas and venter greenish, sheath brown; legs moderately light brown, most of coxae, trochanters, and basal portion of tibiae, straw color; wings clear, veins almost black except costa which is dark brown. General structure typi-

cal for genus. Sheath with scopal pads low and extending almost to the mesal edge of the valve. Lance typical for genus. Lancet (fig. 1) with 11 annuli, the last one sometimes indistinct; annulus 1 extending considerably below level of tractium, almost reaching ventral margin; ventral lobes of annuli 2, 3, and 4 almost equal in size, relatively small but heavily sclerotized and sharply delineated; teeth on annuli 1, 2, and 3 extremely small and numerous, those on succeeding annuli a little larger but much smaller than in described forms of the *virginianus* complex. In general proportions the lancet is unusually long and narrow, the annuli appearing far apart; annuli 2, 3, and 4 are curved and parallel, whereas annulus 1 is straighter, divergent from annulus 2 and approaching a position at right angles to the virga.

MALE.—Length 6 mm. Color chiefly black except for the following parts which are reddish or yellowish: mouth parts, legs, and venter of abdomen. General structure and genitalia typical for the genus.

Holotype female.—Union County, Arkansas, emerged January 10, 1958, reared from *Pinus echinata,* L. O. Warren. *Allotype male.*—Same data. *Paratypes.*—Same data, reared during various dates in January, 112 females, 6 males. Holotype, allotype, and a series of paratypes in the collection of the Illinois Natural History Survey; paratypes in the collection of the Department of Entomology, University of Arkansas, and in the U. S. National Museum.

The larva of this species is unusually dark. In the last feeding stage the head is almost black and the dark bands on the body are sufficiently wide that the mesal and lateral pale areas appear as narrow stripes. Warren (1958) has reported outbreaks of this species in Union County, Arkansas.

This species appears to be a typical member of the *virginianus* complex, differentiated from other species in the complex by the narrower lancet, the wider spacing of the annuli, and the unusually small teeth on the annuli.

Neodiprion merkeli n. sp.

FEMALE.—Length 8 mm. Body and legs brown, dorsum of thorax and central part of head with slightly darker suffusions, lateral lobes of scutum each with a lateral dark stripe; flagellum black; wings with nearly black veins, but with Costa straw color and the stigma with only the edges dark. General structure typical for genus. Sheath with

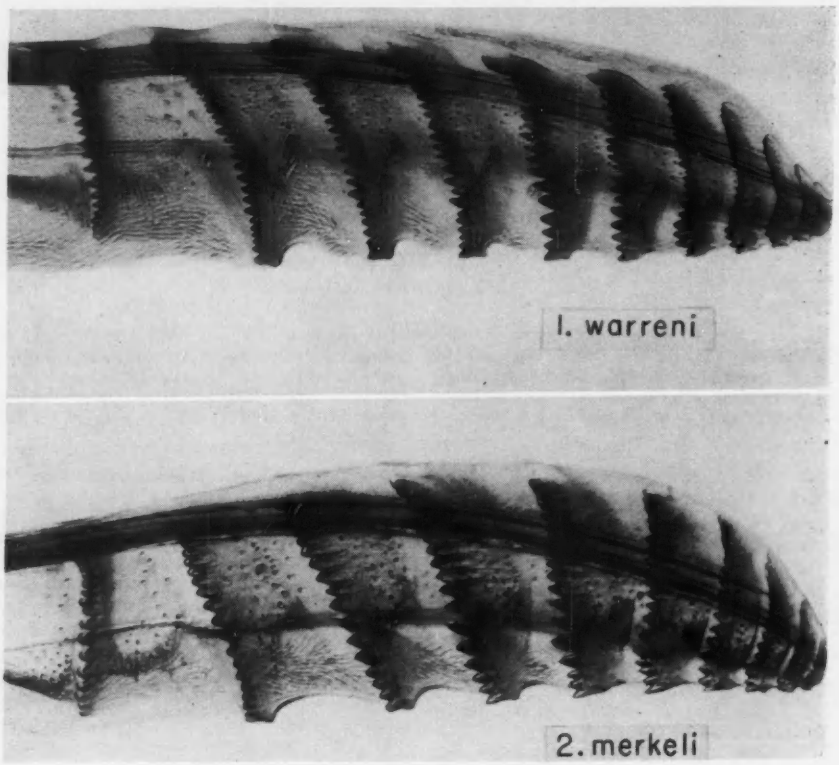

FIG. 1.—Holotype lancet of *Neodiprion warreni.* x 120.
FIG. 2.—Holotype lancet of *Neodiprion merkeli.* x 100.

scopal pads projecting posteriorly as high, thin flanges, the membranous pad of the scopa restricted to the inner vertical face of these flanges. Lance typical for genus. Lancet (fig. 2) remarkably similar to that of *warreni*, with 10 distinct annuli; annuli 2, 3, and 4 parallel, 5 also nearly parallel with 4; annulus 1 greatly divergent from annulus 2, extending below level of tangium and almost reaching margin of lancet; teeth on annuli 1, 2, and 3 numerous and small, some teeth on the other annuli larger but much smaller than typical for either the *virginianus* complex or the *pini-rigidae* complex; ventral tooth of annuli 2, 3, and 4 almost equal, moderately small but well defined.

Male.—Length 6.5 mm. Color black with the following parts yellowish or reddish: mouth parts, basal segments of antennae and areas of head below them, much of pronotum, legs, venter of abdomen, and almost all the venation.

Holotype female.—Fort Myers, Florida, April 22, 1958, *Pinus elliottii* var. *densa*, O. G. Langdon; type no. U.S.N.M. 65064. *Allotype male.*—Same data. *Paratypes.*—Same data, 4 females, 4 males. All associated with Hopkins No. 49161. Holotype and allotype deposited in the U. S. National Museum, paratypes in the Southeastern Forest Experiment Station collection, Lake City, Florida, and in the collection of the Illinois Natural History Survey.

The last larval feeding stage of this species differs from described forms in having the head above the eyes reddish and below the eyes almost a sooty black with a slight reddish suffusion. Mr. Langdon informs me that when rearing it Mr. Merkel identified this species as being unusual and different from species previously reported from Florida.

The affinities of this species are curious. The high flanges on the sheath are typical of the *pini-rigidae* complex, matching those of *excitans* Rohwer with remarkable fidelity. The saw, on the other hand, is quite unlike those found in the *pini-rigidae* complex, in which annuli 2 and 3 are parallel but markedly divergent from annulus 4. The saw of *merkeli* is remarkably similar to that of *warreni*, not only in the juxtaposition of the annuli but also in the unusually small teeth. This combination of characters suggests one of two phylogenetic relationships for *merkeli*. It may be a primitive member representing a form ancestral to the specialized *pini-rigidae* complex. It might also be a species of hybrid origin resulting from a cross between a member of the *pini-rigidae* complex such as *excitans*, which occurs in Florida (Hetrick 1959), and a member of the *virginianus* complex such as *warreni*. If it is of hybrid origin, *merkeli* represents a stabilized hybrid form having a mosaic of distinctive parental characters, reminiscent of the putative hybrid species described in the leafhopper genus *Erythroneura* (Ross 1958).

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Comparison of Mating and Biting Behavior in Two Laboratory Strains of *Anopheles quadrimaculatus*[1]

NATHAN STAHLER[2] AND LEVON A. TERZIAN[3]

Naval Medical Research Institute, National Naval Medical Center, Bethesda, Maryland

ABSTRACT

In order to assemble some evidence of possible physiological differences which have developed among laboratory strains of *A. quadrimaculatus*, and which might lead to biological segregation, a colony from Wilson Dam, Alabama, was compared in detail with another from Bethesda, Maryland. Significant divergence was found in sexual activity, in that the former group mated at lower rates and exhibited a midwinter sexual diapause. The males of both laboratory strains tended to mate with females of their own origin. Biting rates on guinea pigs and chickens were also markedly different, the Wilson Dam groups again being less active. In the third year of studies the two strains converged in these behavior patterns. No significant differences were found in other aspects of life history and morphology.

These studies were initiated in order to determine if a midwinter sexual diapause which had been noted in the laboratory colony of *Anopheles quadrimaculatus* Say at the Naval Medical Research Institute (Stahler 1959) would also be a characteristic trait of this species from other areas. Preliminary comparisons with a laboratory strain of *quadrimaculatus* obtained from the TVA showed that biological differences existed between the two colonies. Consequently, these investigations were extended to include life-history studies other than mating, with a view towards establishing some of the means by which subspecific categories arise and segregate. Such information is of considerable importance in the epidemiology and control of mosquito-borne diseases.

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[2] Entomologist.
[3] Parasitologist.

MATERIALS AND METHODS

The colony of *Anopheles quadrimaculatus*, which has been continuously inbred at the Naval Medical Research Institute since 1945, is herein designated as the "N" laboratory strain. Some of the biological characteristics of this strain have been previously reported (Stahler 1959). The colony was established from ova received from the USDA laboratory at Beltsville, Maryland, which, in turn, was a mixture of colonies from the Rockefeller Foundation Station at Tallahassee, Florida, received in 1942 via 3 years at the USDA laboratory in Orlando, and from the same Orlando colony, received in 1944 from Merck & Company at Rahway, New Jersey, where it had been in culture for 1 year.

In March, 1957, *quadrimaculatus* ova were obtained from the TVA laboratory at Wilson Dam, Alabama, through the courtesy of the late W. E. Snow. This colony, designated as the "T" laboratory strain in this report, has been described by Crowell (1940) and was established in 1937 from ova obtained from the Tallahassee laboratory where it had been cultured for 5 years. In 1950-52 it was supplemented with collections of wild-caught mosquitoes from west Tennessee. It is therefore evident that, for the most part, the two strains of *quadrimaculatus* to be reported upon in these studies were sympatric. They have been allopatric since 1937 under the influence of selective factors operating in widely separated laboratories. For example, it may be noted that at Wilson Dam, the "T" strain was reared at 75° ± 2° F., while the "N" strain was maintained in Bethesda at 80° ± 1° F. Moreover, the former was routinely fed on rabbits, the latter on guinea pigs.

For lack of a better term, these populations are characterized as "strains". This is meant to imply that certain physiological differences have been demonstrated, but neither genetic isolation nor any morphological divergence has been found. It is similar to a "biotype" as used by Bates (1940) and may represent one manifestation operating in the creation of a sibling species.

The methods of anopheline culture and the physical characteristics of the NMRI insectary have been previously described (Stahler 1959). Under these conditions, approximately 18 generations of *quadrimaculatus* have been produced annually. In August, 1958, the mosquito colonies were remvoed to another room, which was maintained at the same temperature and humidity (80° F.; 70%-75% R.H.), but without natural illumination, so that mating had to be stimulated each evening by gradually decreasing the intensity of the room illumination until there was complete darkness and then reversing the process each morning. This was accomplished by a series of incandescent lamps regulated by a clock mechanism in conjunction with the overhead room fluorescent lights, which in turn were controlled by a timer on a 12-hour-on 12-hour-off cycle.[4] Whenever the change from one laboratory room to the other occurred during the course of an experiment and such transfer could have influenced the experimental results, this has been noted.

[4] Designed and constructed by M. Eicher, Head, Instrumentation Laboratory, NMRI.

RESULTS

Oviposition.—The oviposition habits of the two strains were compared by individually isolating inseminated females which had taken a blood meal from chickens and recording the eggs subsequently deposited in Stender dishes. Since few females could be induced to take a second blood meal after the primary oviposition had been completed, the observations were limited to the results obtained with a single blood meal.

In the N females, 48 deposited viable, fertile eggs (usually 90%-100% hatch, rarely less) and 6 laid only infertile eggs. Ten females did not oviposit, although they contained fully developed ova. No oviposition occurred in any noninseminated female. In similar observations with the T strain, 53 females deposited fertile eggs (with the same percent hatch as in the other group), but none laid only infertile eggs. Eleven females failed to oviposit, in spite of the fact that they were replete with fully developed ova. One female oviposited with no evidence of having been inseminated.

Based on the normal probability curve, the differences between the two strains in the proportions of females depositing only infertile eggs were significant at the 5% level. This suggests a divergence in the ability to retain unfertilized ova, but the numbers of individuals involved preclude conclusive evidence.

In the N strain, the median number of fertile eggs laid per female was 203, with a range of 9 to 360; in the T group the median was 201, with a range of 49 to 336. Forty-seven N females began oviposition on the second night after the blood meal, one on the third night and none thereafter. In the T strain, 47 females began to lay eggs on the second night, 5 on the third, 1 on the fourth, and none thereafter. Of those females which oviposited during more than one 24-hour period, two were in the N group and three in the T. It is evident that no real differences have developed between the two strains in oviposition habits. Furthermore, no morphological differentiation could be discerned in the eggshells and floats, which are the structures usually involved in subspecific segregation of mosquitoes.

Larvae.—The relative adaptability of both larval strains to the laboratory temperature, diet or other factors involved in rearing techniques was tested for significant differences. For this purpose, 14 larval colonies of each strain were set up on the day of hatching in white enameled pans (7" diam.) containing 200 cc. tap water. Each colony, consisting of 50 individuals, was fed with equal amounts of powdered dog food until pupation was complete. Under these experimental conditions, the larval periods of 208 N males and 245 N females were 10.9 ± 0.99 days (mean and standard deviation) and 11.4 ± 1.19

days, respectively. In the T strain the comparable data were 11.0 ± 1.19 days for 238 males and 11.7 ± 1.19 days for 237 females. According to the chi-square test for homogeneity between distributions, the differences in larval developmental time between the strains were not significant. However, the differences in larval periods between sexes were significant in both strains, in that the males usually pupated earlier. In the N strain, the chi-square value was 24.68 at 5 d.f. and in the T strain 42.82 at 5 d.f. The T strain did not, therefore, deviate from this well-known characteristic, previously reported in the N strain (Terzian and Stahler 1949).

In both strains the numbers of male and female larvae surviving to pupation were similar. Altogether, 65% of the N larvae and 73% of the T larvae completed development. No further differences in larval behavior or development were observed. During the years 1957 and 1958, the T larval colonies contained more dark, melanotic individuals than did the N strain. However, in 1959 and 1960 these differences were no longer apparent and it may be surmised that they were eliminated by selection.

Adult Longevity.—Both strains were observed during the spring of 1958 for evidences of any differences in adult longevity. The survival rates of 20 imagoes of each sex, isolated in 10 replicated groups, yielded, in summary, the following results (means and standard deviation). In the N. strain, 192 males lived for an average of 22.5 ± 9.9 days and 191 females for 24.7 ± 7.3 days. In the T groups, 191 males survived 24.5 ± 9.5 days and 197 females for 26.2 ± 7.8 days. The patterns of the survival rates were analyzed by the chi-square test for homogeneity of frequency distributions and it was established that, (1) in both strains there were significant differences, but only at the 5% level, between sexes in adult survival rates, and (2) the similar differences noted between N and T males or N and T females were of the same borderline level of significance. These results do not warrant a definitive conclusion with respect to any differences in adult longevity of the two strains.

Sexual Activity.—The sexual behavior of mosquitoes under laboratory conditions has been shown to be of value in distinguishing subspecific categories, since characteristic differences have been observed in their degree of stenogamy. These two strains of *quadrimaculatus* were compared in this respect for a period of 28 months, from April 1957 to March 1960, by permitting 4-8 experimental groups each month (total 576) to cohabit for the first 10 post-emergence days and then determining the number of females from each group which had been inseminated. The monthly average rates of insemination for the two strains, in homologous and heterologous populations, are presented graphically in figures 1 and 2 and summarized in table 1, in which the means with standard deviation are given for the three separate periods of observations.

These data, after being subjected to analyses of variance, with Duncan's method of mean separation, elicit these conclusions. Figure 1 indicates that the rate of insemination in the N groups consistently remained at a high level (about 92%) during the experimental periods and, in fact, showed no change from the results obtained in a study several years earlier (Stahler 1959) which had demonstrated the disappearance of a diapause in sexual activity. The uniform sexual activity during the three arbitrarily selected periods of observations (94%, 91% and 94% insemination, respectively) is further demonstrated in table 1.

In contrast, in the homologous groups of the T strain, the percent inseminated females increased perceptibly in 1959-60 from what it had been in 1957-58. For all monthly mean rates, the F value (5.06, significant at 27 and 127 d.f.) indicated that differences between months were greater than within replicates. Two significant changes in sexual activity occurred—initially, in the increase of mating from April 1957 (58%) to the following June (83%) and secondly, from July 1957 (80%) to November and December of the same year (47% and 58%), with a recovery of activity in March 1958 (73%). The latter decline in insemination during the winter months may be compared to similar behavior found in the N strain in 1949 to 1953, but apparently the T strain became acclimated more rapidly than had the N strain, since no such diapause was found during the next two winters. A summary of the rates of insemination in table 1 shows that mating activity in April 1957 to July 1958 (69%) was significantly lower than in the two following periods (82% and

Table 1.—The mean rates of insemination, with standard deviations, during three periods of observations of two strains of *A. quadrimaculatus* in homologous and in heterologous populations.

Male	Female	Mean rate of insemination during period stated		
		IV/57 - VII/58	X/58 - III/59	X/59 - III/60
N	N	93.6 ± 7.6	91.4 ± 9.0	93.8 ± 6.1
T	T	69.2 ± 17.3(a)	82.5 ± 12.9(b)	91.4 ± 7.0(b)
N	N	67.9 ± 15.9(c)	84.5 ± 9.5(d)	85.3 ± 7.6(d)
T	T	81.5 ± 14.4(e)	90.5 ± 9.3(f)	91.3 ± 7.4(f)

(a, b); (c, d); (e, f) Differences of means significant (1%).

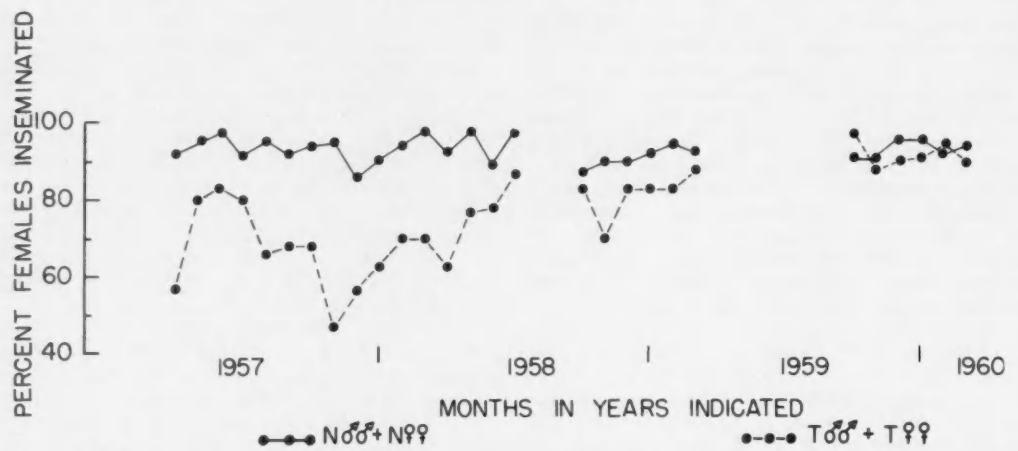

FIG. 1.—The average monthly percent inseminated females of the N & T strains of *A. quadrimaculatus* in homologous populations.

91%). The rates of insemination of the T groups were significantly lower than those of the N groups from April 1957 to July 1958 and from October 1958 to March 1959, but similar from October 1959 to March 1960.

Previous studies of seasonal changes in the mating activity of the N laboratory strain, had shown that early mortality of the male mosquitoes probably had been a factor in sexual diapause, but inspection of such survival data in the experimental groups of the T strain showed that male mortality could not have been a determining influence in these experiments, as it was constant throughout, even in November 1957. Consequently, more subtle factors, not readily evident, must have been involved in the sexual diapause noted.

The third series of experimental groups consisted of heterologous populations of N males and T females. No real differences were found in mating activity between these groups and the homologous T populations (table 1) but, as illustrated in figure 2, the N males-T females groups mated at consistently lower levels than did the homologous N groups, but with less differences in 1958-60. The analysis of variance of the data shown in figure 2 yielded an F value of 5.90 at 27 and 107 d.f., indicating heterogeneity in mean monthly rates of insemination, with a significant change in mating activity in November 1957 (42%) as contrasted to that which had occurred in the previous month (60%) or in 2 months later (70%). Such diapause, as noted above, occurred at the same time in the homologous T groups. The mean rates of insemination of this third series, like that of the second, were significantly lower in April 1957 to July 1958 (68%) than in October 1958 to March 1959 (84%) or in October 1959 to March (85%).

Further conclusions may be drawn from the data supplied by the fourth series, T males and N females. An analysis of the data presented in figure 2 yielded an F value of 5.48 at 24 and 110 d.f., indicating heterogeneity between months, with a significantly low level of mating activity in November 1957 (71%) and in January 1958 (72%). Again, this was during the same period of reduced sexual activity found in the homologous groups of the T strain. The mating activity during the first period of observations (table 1) was 82%, or less than that found subsequently, indicating that acclimatization proceeded at about the same rate in both sexes of the T strain. From 1957 to the latter part of 1959, the experimental groups of this series mated less actively than did the homologous T groups, but subsequently the rates of insemination of both series were similar. On the other hand, the rates of insemination of the groups consisting of T males and N females equaled those of the homologous N strain at the beginning of 1959 or about 9 months earlier than they had become similar to the T groups.

A comparison of the rates of insemination during the period April 1957 to July 1958, when acclimatization of the T groups was in progress, showed that there were significant differences between the monthly mean rates in the four series ($F = 28.7$ at 3 and 56 d.f.). The homologous N groups mated at higher levels than did the others, the T males and N females series were second in activity and the two series containing T females were at the lowest level of sexual activity. This suggests that the female of each strain played a greater role in determining the degree of sexual activity.

Cross-mating.—The possibility of genetic barriers to interbreeding was investigated by permitting males to cohabit with equal proportions of females of both strains and then ascertaining whether or not preferential mating had occurred. For this purpose, 20 females of one strain were lightly covered with gold dust and released into a cylinder containing 20

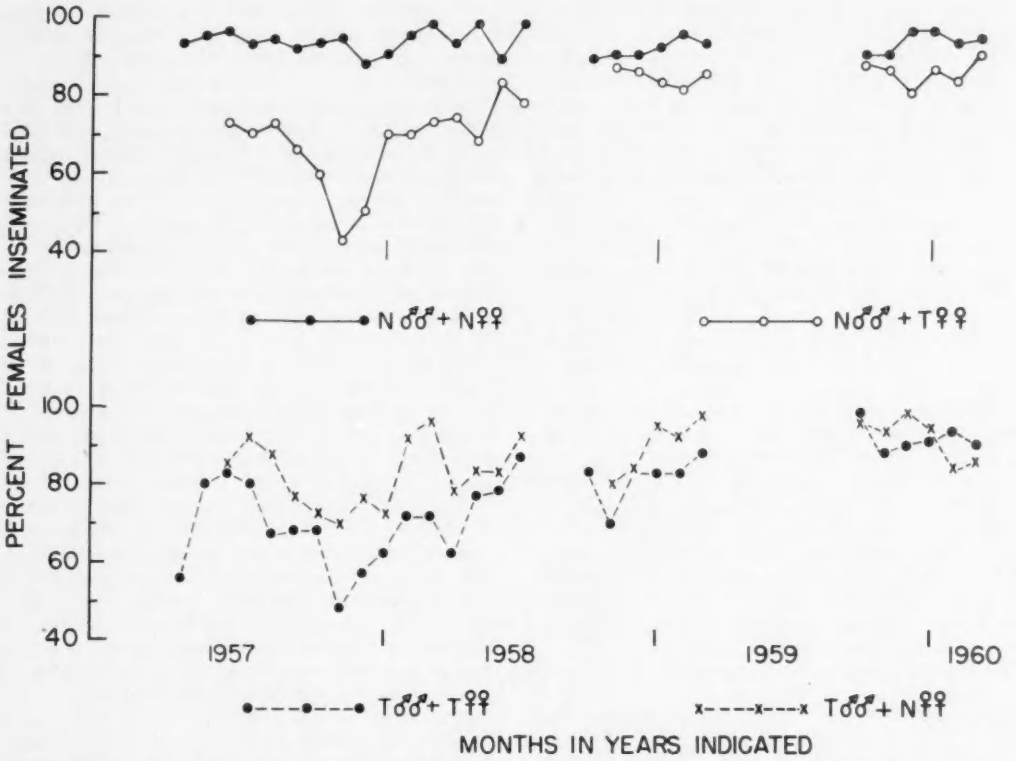

FIG. 2.—The average monthly percent inseminated females of the N & T strains of *A. quadrimaculatus* in homologous and heterologous populations.

undusted females and 20 males of the same or the other strain, all 4 days old. Cohabitation was permitted for 24 hours, at the conclusion of which period all 40 females were dissected for evidence of insemination. This procedure was replicated 10 times for each of the two strains of males. The mean rates of insemination, with variance, of the dusted and nondusted females of the same strain proved to be subequal, indicating that such dusting had no discernible effect on successful completion of mating under these experimental conditions. Accordingly, the data for dusted and nondusted females were treated as 20 experimental replicates.

In order to determine whether either strain of males mated preferentially, it was necessary to first establish the mating propensity of the males with homologous populations of females. This data, shown in table 2, indicates that the male N mated at significantly greater rates with the female N (70%) than with the female T (44%), when not offered a choice between the two. The male T, however, mated equally well (about 48% insemination) with both strains of females. Differences were analyzed by the standard error of the differences between means.

In the concomitant experiments, the males were offered a choice of mating partners. In heterologous female populations, both strains of males mated in expected proportions with the N females. Thus, 70%

Table 2.—The mean rates of insemination, with standard deviations, resulting from 24 hours cohabitation of each strain of males with the two strains of females, either in homologous (expected rates) or in heterologous (observed rates) populations.

	Expected rates (%)*			Observed rates (%)*		
Males	Female N	Female T	P	Female N	Female T	P
N	70.5 ± 8.4	44.0 ± 11.2	.0001	73.0 ± 7.5	58.0 ± 10.5	.0003
T	48.2 ± 9.2	48.0 ± 10.7	—	49.8 ± 9.0	66.8 ± 12.0	.0002

* Differences between expected and observed rates significant (P=.005) in Male N + Female T and in Male T + Female T.

were inseminated by the N males and 50% by the T males. But in the same heterologous female populations, both strains of males mated in significantly greater proportions with the T females (chi-square = 91.05). The N males inseminated 58% of these females and the T males mated with 67%. The results of these experiments do not offer a ready explanation for the differences between expected and observed rates of insemination. The males were able to select their mating partners and evidently preferred females of their own strain, since they mated with such strain of females as well or better in heterologous populations than when the latter were in homologous groupings. In heterologous populations, the differences in rates of insemination between strains were significant at the .03% level for the N males and .02% for the T males.

Apparently, no practical barriers to complete "hybridization" developed, even though there was a significant degree of preferential mating. Since these experiments were conducted in the summer and fall of 1959), they must be evaluated according to the length of time the T strain had been in cultivation at the NMRI. Inspection of figure 1 suggests that the T strain was less stenogamic during the previous year and during that period the male T may, in a heterologous female population, have inseminated the N strain of females with even less facility.

Interfertility.—The most significant indication of the degree of isolation between populations is in the measure of their interfertility. When N males were mated with T females or when T males were mated with N females, the results indicated that no effective genetic barrier had arisen to prevent complete "hybridization" between the two strains. From either cross, in the F-1 generation egg production and viability, larval growth and pupation, and eclosion of the imagoes were the same. Similarly, the F-2 generation gave no indication that any degree of sterility had developed. In view of these results, such data were not accumulated for subsequent generations.

Biting Rates.—Possible differences in blood avidity of these two laboratory strains of mosquitoes were determined by exposing them to guinea pigs and chickens during several intervals over the 3-year period. In order to establish the biting rates on guinea pigs, 20 experimental groups, each consisting of 20 5-day-old virgin females, were dark adapted for 90 minutes and then allowed to feed in darkness on the shaven back of a tightly secured white male guinea pig, weighing about 800 grams. Technical difficulties prevented the use of the same procedure with chickens, so that for these animals, the mosquitoes, also in 20 experimental groups, were adapted at 10-17 foot-candles for 7 hours, following which, 400-gm. chickens, plucked on the exposed side, were secured onto the cylinders housing the mosquitoes and left in such position for 20 minutes. The maximum light intensities were 11.0 ft. cds. in the center of the cylinder and 1.4 ft. cds. at the biting surface. Regardless of the degree of engorgement, all mosquitoes containing blood were considered to have fed.

The data from these experiments, presented in table 3, indicate that the difference in biting rates between the strains were significantly different in 1958 and in 1959, but not in 1960. During the period from April through October, 1958, 49% of the N females, in contrast to 19.6% of the T females, fed on the guinea pigs. However, in the period beginning 13 months later, from November, 1959, through January, 1960, the differences between the two strains were no longer significant. While 52.0% of the N females took blood, the biting rates of the T strain had increased to 43.5%. In neither comparative test was there a significant difference between variances. Similar results were obtained by using chickens as host animals. In the first experimental period, October, 1958, through January, 1959, 65.5% of the N females and 32.9% of the T took blood, a highly significant difference. In the second period, which began 12 months later and lasted through February, 1960, the biting rates of the two strains were similar, 72.6% for the N and 66.8% for the T. Again, there was no real differences in the variances.

These results indicate that the biting propensity of the T strain increased progressively with continued cultivation in these laboratories. Since the T strain had been previously adapted to feeding on rabbits, it might be expected that its biting rates on guinea pigs and chickens would initially be low. The continuous use of guinea pigs as the sole source of blood for oviposition purposes would probably enhance the propensity of the mosquitoes towards these animals. Laarman (1958) concluded that *Anopheles atroparvus* became adapted to rabbits after 20 laboratory-

Table 3.—The mean percentages, with standard deviations, of *quadrimaculatus* females, feeding on guinea pigs or chickens during various periods of observations.

Period	N Strain		T Strain	
	Guinea pig	Chicken	Guinea pig	Chicken
IV/58-X/58	49.4 ± 19.1(a)		19.6 ± 17.7(b)	
IX/58-I/59		65.6 ± 14.6(c)		32.9 ± 12.8(d)
XI/59-I/60	52.0 ± 27.1		43.5 ± 26.5	
I/60-II/60		72.6 ± 12.8		66.8 ± 15.2

(a, b); (c, d) Significant difference at 1%.

bred generations. The results with *quadrimaculatus* would tend to corroborate his findings. However, a concomitant increased avidity for an entirely different host—namely, an avian one—would suggest that the general vigor of the T strain had increased and that adaptation towards guinea pigs was not the sole factor in explaining the increased biting rates on these animals.

COMMENT

Considerable information has been gathered concerning the taxonomy of the *Anopheles maculipennis* complex, of which *quadrimaculatus* represents an important, although somewhat aberrant, member. Subspecific categories of *quadrimaculatus* have not as yet been recognized. Hinman (1936) was unable to warrant the establishment of a subspecies based on hibernation requirements, and Coggeshall (1941) found an inheritable color pattern in the larvae and pupae, but no other morphological or physiological differentiation.

The studies reported in this paper indicate that some subspecific divergence in *quadrimaculatus* may occur by cultivation of microgeographical populations. Such segregation, occurring initially in biting rates and epigamic activity, but not in life cycles, interfertility or polymorphism, indicates to some extent the pathways by which geographical races may be established. Rozeboom and Gilford (1954) suggested that differential sexual activity was the means by which the strains of the *Culex pipiens* complex maintained their identity in nature, and Roubaud (1948) differentiated races of *Anopheles claviger* with respect to their mating ability in cages.

Since ecological preferences cannot be properly evaluated in the laboratory and no rigid genetic barriers were demonstrated, the "N" and "T" populations of *quadrimaculatus* must be considered only as discrete laboratory strains. But geographical speciation is always preceded by the origin of potential isolating mechanisms, which will be improved by natural selection and the observations which indicate that preferential mating exists between the two strains strongly suggest that reproductive isolation may yet occur.

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SCIENTIFIC NOTES

Comparative Elimination of Radiocesium and Radiostrontium by Grasshoppers[1]

D. A. CROSSLEY, JR., AND JAY H. SCHNELL[2]

Health Physics Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee

Recent entomological investigations have proved the value of radioactive isotopes as research tools in varied studies ranging from physiological problems to insect control (Jenkins 1957). In areas contaminated by radioactive waste products, radioisotopes are providing information on the position and importance of insects in the transfer of materials through communities (Crossley and Howden, unpublished data). In a contaminated radioactive area (White Oak Lake bed) at the Oak Ridge National Laboratory, Oak Ridge, Tennessee, a difference in the relative accumulation of Strontium-90 and Cesium-137 by insects was found: Insects reached equilibrium concentrations for Cesium-137 which were almost as high as concentrations in the plants, but Strontium-90 concentrations in the insects were nearly an order of magnitude lower than the corresponding plant concentrations. Laboratory studies on the elimination of radioactive isotopes of cesium and strontium by grasshoppers provided an explanation for this difference.

The rate of elimination of an isotope by insects is proportional to the concentration in the insect body:

$$\frac{dA_t}{dt} = -\lambda A_t \qquad (1)$$

where A_t is the radioactivity in the insect at time t and λ, a constant, is ln. $0.5/T_b = 0.693/T_b$. T_b is the biological half-life and is defined as "the time taken for the amount of a particular element in the body to decrease to half its initial value due to elimination by natural (biological) processes". The concentration in the insects as a function of time is given by:

$$A_t = A_o e^{-\lambda t} \qquad (2)$$

where A_o is the initial radioactivity and t is elapsed time. This equation assumes no further ingestion of isotopes by the insects and thus is useful primarily in describing the loss of radioactivity by insects following single feedings of radioisotopes under laboratory condi-

[1] Research performed in the Health Physics Division of the Oak Ridge National Laboratory, operated for the U. S. Atomic Energy Commission by Union Carbide Corporation. Accepted for publication October 7, 1960.

[2] Present address: Department of Zoology, The University of Georgia, Athens, Georgia.

tions (Crossley and Pryor 1960). The constant λ, however, is a parameter which may determine the value of the equilibrium reached by the insects under field conditions (Davis and Foster 1958). In these studies, concerned primarily with Strontium-85, Strontium-90, and Cesium-137, the biological half-lives, T_b, are relatively short compared with the radioactive half-lives, T_r, and no correction need be made for T_r. In the general case, however,

$$\lambda = \lambda_r + \lambda_b \quad \text{or} \quad T = \frac{T_r + T_b}{T_r T_b}.$$

In this study, since $T_b \ll T_r$, $T = T_b$.

Experimental methodology was as follows: Adult grasshoppers, *Melanoplus differentialis* Thom. and *M. femur-rubrum* (DeG.),[3] were allowed to feed upon grass leaves smeared with Strontium-85 or Cesium-137. The grasshoppers were counted for radioactivity immediately after the initial feeding, so that subsequent counts could be expressed as a percentage of the initial count. A model 810 Baird-Atomic gamma scintillation detector with a 2 x 2-in. well-type crystal was used for the estimates of gamma radioactivity. Counts were made at 4- to 8-hour intervals, depending upon the requirements of the experiment. During the experiments the grasshoppers were fed fresh, uncontaminated grass or kudzu [*Pueraria lobata* (Willd.)] leaves.

Results of the experiments with Strontium-85 and Cesium-137 in *Melanoplus differentialis* showed that strontium was eliminated much more rapidly than was cesium. Figure 1 illustrates the elimination of Cesium-137 by this grasshopper species. Elimination of cesium proceeds at a rate corresponding to a biological half-life of about 2 days. In contrast, Strontium-85 was eliminated with a shorter biological half-life of about 12 hours (fig. 2). Similarly, for *Melanoplus femur-rubrum*, biological half-lives were approximately 30 hours for Cesium-137 and 10 hours for Strontium-85 (fig. 3).

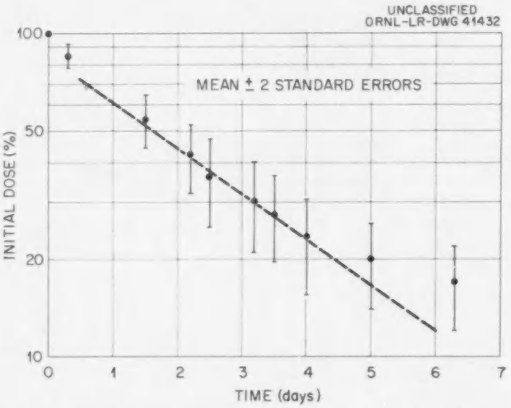

FIG. 1.—Elimination of Cesium-137 by *Melanoplus differentialis* Thom.

The more rapid elimination rate for Strontium-85 as compared with Cesium-137 explains the previously mentioned difference between the equilibrium concentrations for these elements under field conditions. Cesium, being

[3] We thank Dr. Theodore H. Hubbell, University of Michigan, for the identification of *Melanoplus femur-rubrum*.

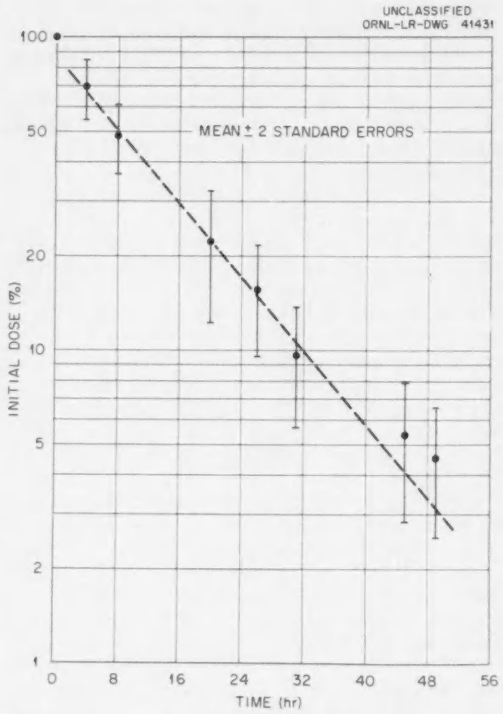

FIG. 2.—Elimination of Strontium-85 by *Melanoplus differentialis* Thom.

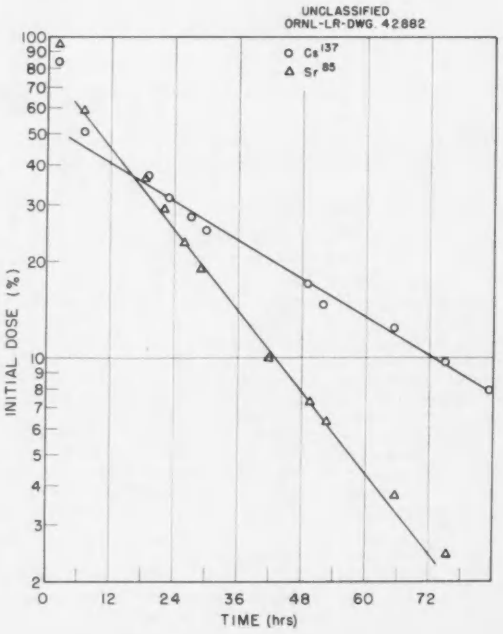

FIG. 3. Elimination of Cesium-137 and Strontium-85 by *Melanoplus femur-rubrum* (DeG.). Values shown are means for 6-8 specimens.

eliminated less rapidly than strontium, would tend to build up higher concentrations relative to strontium before loss was balanced by intake. The differences in the parameter λ are enough to explain why the insect-to-plant ratio for Cesium-137 was higher than the insect-to-plant ratio for Strontium-90.

Noteworthy also is the fact that the smaller species of grasshopper eliminated both isotopes more rapidly than did the larger one. A previous report (Crossley and Pryor 1960) dealt with *Romalea microptera* (P. de B.), which is a still larger grasshopper; in this case a longer (4-5 day) biological half-life for Cesium-137 was reported. (No experiments using strontium have been performed with *Romalea microptera*.) Thus the rate of elimination appears to increase with decreasing size of the insect. Similar results for mammals were reported by Richmond (1958).

The last points on the curves in figures 1-3 fall above the lines, suggesting that a longer-component elimination rate is also present. For purposes of comparison of the two isotopes, it seems adequate to use a single exponential as in Equation (2) to represent elimination. For more critical evaluations of the cycling of isotopes in field situations, it may be necessary to express elimination rates by the use of more than one component.

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Vidia (Coleovidia) cooremani, New Subgenus and New Species, and Notes on the Life History (Acarina: Saproglyphidae)[1]

H. A. THOMAS[2]

Texas A. and I. College, Weslaco, and
Texas Agricultural Experiment Station, Weslaco

In a study of the predaceous ladybeetle *Chilocorus cacti* L., the author found hypopi of a previously undescribed mite, *Vidia* sp., frequently associated with the insect. Mites of the family Saproglyphidae have usually been found associated with wasps. However, Atkins (1959) has reported mites of this genus associated with the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk. Certain details of the life history of the mite found by the author, together with a description of the hypopus, are given here.

METHODS AND MATERIALS

From April through November 1958, collections of the ladybeetle *Chilocorus cacti* were taken from a citrus orchard near Weslaco, Texas, at 10-day intervals. The beetles were collected by tapping the limbs and foliage, and were stored in vials of alcohol. During dissection of the beetles for sex determination, mites were found attached to the inner lining of the elytra on many of them. Records were taken on the number of mites present, and specimens were mounted for species determination. In 1959, further collections of beetles taken from other areas in the lower Rio Grande Valley were studied, and other life stages of the mite were sought in the field.

Vidia, subgenus **Coleovidia,** new subgenus

Coleovidia, type *V.* (*C.*) *cooremani*, new species, is separated from the other two subgenera in this genus by having only one large, lanceolate seta on tarsi I and II. *Vidia*, s. str., possesses three, and subgenus *Crabovidia* has two such setae.

Vidia (Coleovidia) cooremani, new species

Adults.—Not known.

Hypopus (fig. 1).—Broadly oval; dorsal setae short. Eyes closely set, as shown in figure 2. Gnathosomal

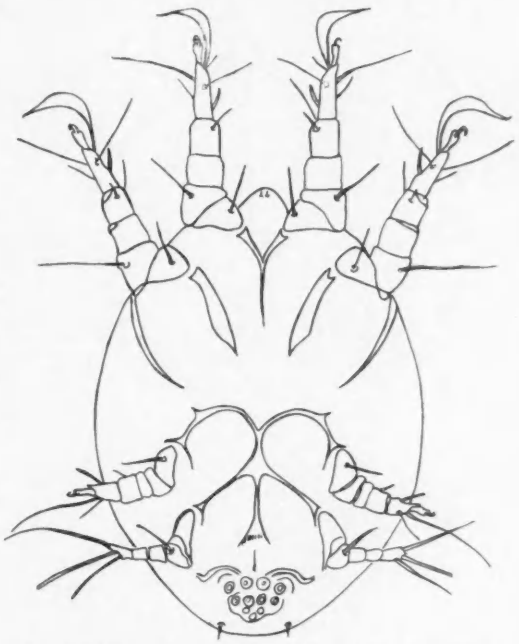

FIG. 1.—Hypopus of *Vidia* (*Coleovidia*) *cooremani*, ventral view.

setae very short. Apodemes of coxae I and II as figured; those of coxae III rounded; those of coxae IV straight, forming more than a 90° angle with each other. Suctorial plate small, as figured. Legs short, stout; setal pattern as figured (fig. 3). Sensory rod of tarsus I long, slender, enlarged slightly distally; that of tarsus II tapering to distal end. Legs I, II, and III each with pretarsus and clawlike empodium; tarsus IV without pretarsus or empodium, with two long and one short setae. Length of holotype 236μ, width 178μ.

The holotype (U. S. National Museum No. 2596) was collected on *Chilocorus cacti* L., at Weslaco, Texas, July 19, 1958 (H. A. Thomas). Three paratypes were collected on the same host and at the same locality, but on June 10, October 23, and November 5, 1958. All are in the U. S. National Museum collection.

LIFE HISTORY

The hypopus occurs in close association with *Chilocorus cacti* adults or the pupal exuviae of that beetle. *C. cacti* occurs commonly on citrus throughout the

[1] Accepted for publication October 13, 1960.
[2] Present address: Maine Forest Service, Augusta, Maine.

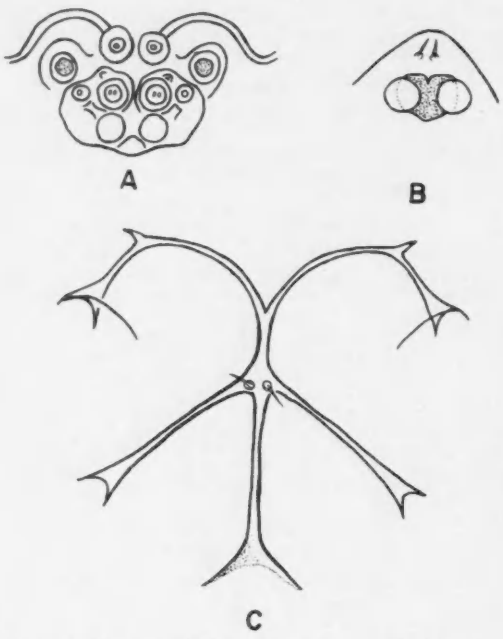

FIG. 2.—Hypopus of *V. cooremani*. A, anal plate; B, head; C, apodemes of coxae III and IV.

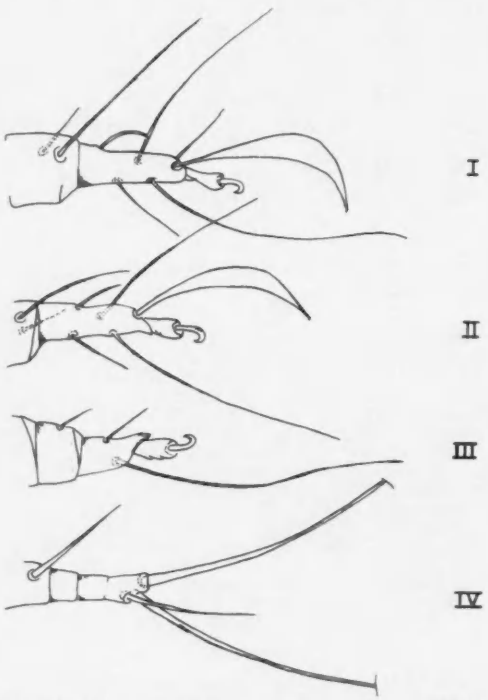

FIG. 3.—Hypopus of *V. cooremani*; tarsi I through IV.

lower Rio Grande Valley of Texas. On the adult insect, the hypopi are found under the elytra, particularly along the inner surface of the epipleura. Figure 4 shows a cluster of mites on a detached elytron. In the field, the mites were found crawling among the pupal exuviae of the beetle, but their habits in this instance were not studied further.

The mites were found to be most numerous in the spring and fall, with the lowest average number of mites per beetle occurring in the summer. Figure 5 illustrates the trend of the average number of mites per beetle during 1958. One female of *C. cacti* collected on November

FIG. 4.—Internal view of elytron from lady beetle *Chilocorus cacti*, showing attached clusters of hypopi (arrows) of *Vidia cooremani*.

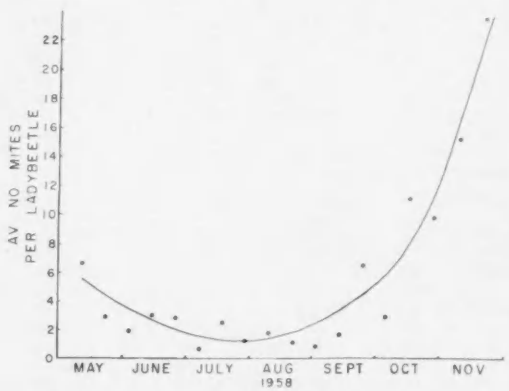

FIG. 5.—Population trend of infestation of *Chilocorus cacti* by *Vidia cooremani*.

19, 1958, had 62 hypopi under one elytron and 40 under the other. This was the highest number recorded.

Examination of 258 beetles collected during the 1958 season showed a higher average number of mites per beetle on females than on males, the averages being 4.7 and 2.7, respectively. The female of *C. cacti* often returns to the clusters of its pupal exuviae to lay its eggs. Since the mite has been found infesting the pupal exuviae, the return of the female beetle to this site provides additional opportunity for her to become infested.

The data on the number of mites per beetle during 1958 (fig. 5) and the percentage of beetles infested during that period were tested for correlation. A significant correlation was found to exist, $r = 0.74^{**}$ (16 df), significant at the 1% level.

Collections of *C. cacti* taken at the following locations, at the times noted, were examined for mites: orange orchard opposite Texas A. & I. College, Weslaco, May-December 1958; Jones-Collier grapefruit orchard, 2 miles southeast of Weslaco, February 1959; Briscoe grapefruit orchard, N. Adams Gardens, March 1959; Kutzenberger orange and grapefruit orchard, Harlingen, March 1959; orange orchard (owner unknown), 4 miles northwest of Mission, June 1959. These collections are distributed in the major citrus producing area of South Texas, and suggest that the mite occurs throughout the region wherever the beetles are found.

No effects of the mite on the beetle host could be detected, either from dissections or from observations of the living beetles. Atkins (1959) reported no effect on the natural flight response where adults of *Vidia* sp. occurred on the Douglas-fir beetle.

ACKNOWLEDGMENTS

The valuable assistance of Dr. E. W. Baker, U. S. Department of Agriculture, Insect Identification and Parasite Introduction Branch, in describing the species and preparation of figures is gratefully acknowledged.

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Effects of Parental Age on Offspring from Isolated Pairs of the Mealworm *Tenebrio molitor*[1]

DANIEL LUDWIG AND CARL FIORE

Department of Biology, Fordham University, New York 58, N. Y.

Tracey (1958) and Ludwig and Fiore (1960) found that at 25° and 20° C. larvae of the mealworm, *Tenebrio molitor* Linn., from young parents grew at a slower rate, required a significantly longer time to complete development, and had more molts than those from old parents. At these temperatures, an increase in parental age resulted in a decrease in the duration of adult life. Ludwig and Fiore (1960) observed that the shortening of the larval period and the reduction in the number of larval molts associated with an increase in parental age were not evident until the parents had aged at least 4 weeks, and the shortening of the adult stage until they had aged 6 weeks or longer. These experiments were performed with beetles of known age from mass cultures using eggs collected at intervals of 2 weeks throughout the egg-laying period (9 to 12 weeks). Since only the beetles which survived 2 months could provide eggs for the oldest parental age groups, possibly selection may be a factor in determining these results. For this reason the experiment was repeated at 25° C., using offspring from isolated pairs of beetles.

MATERIAL AND METHODS

Isolated pairs of newly emerged beetles were kept in chick-growing mash in 50 ml. beakers maintained at 25° C. Moisture was provided by covering the mash with a damp cloth, which was moistened several times a week. After several days each pair of beetles was placed in a separate dish containing white flour and kept at 25° C. A bottle of water, plugged with moist cotton, was placed in each dish. Eggs were collected daily, by sifting the flour, for a period of 4 days. The beetles were then returned to the proper beaker and left there until the next collection period. This process was repeated at intervals of 2 weeks until the end of the oviposition period. The age of the parents was always calculated from the day of emergence.

The eggs were placed in humidifiers over a saturated solution of NaCl (relative humidity, 75 percent) and kept at 25° C. Newly hatched larvae were placed individually in 4-dram vials with a small amount of chick growing mash, and kept at 25° C. in containers with dishes of water to maintain a high humidity. They were kept under these conditions until 1 week after the molt to the fourth instar (5 to 6 weeks) and then a drop of water was added directly to the food three times a week throughout the remainder of the life cycle. Observations were made daily to determine whether the insect had molted, to remove the exuviae, and to provide food and water as needed. Determinations were made on the duration of each stage and on the number of larval molts. The first 10 larvae from each parental age group were weighed at 12 weeks to determine the effect of parental age on size and hence on the rate of growth.

RESULTS AND DISCUSSION

A sufficient number of larvae were obtained from four pairs of beetles. However, since the results from each pair were similar, only those from the pair which produced the most offspring are presented in table 1. In this table, parental age means the age at the beginning of each egg-collection period. Larvae obtained after the parents had aged 1 month or longer grew at a faster rate than those produced earlier. Those from the first and second parental age groups weighed approximately 10, from the third 32.4, and from the last 67.0 mg. at 12 weeks.

The duration of the larval period decreased with an increase in parental age, from 146.1 in larvae from the first eggs to 111.1 days in those from eggs laid 76 days after emergence. No significant difference (difference divided by its standard error is 2 or more) was found in the duration of the larval period until the parents had aged 1 month. The number of larval molts also decreased with an increase in parental age from 13.3 to 11.8. There was no parental-age effect on the duration of adult life. However, because of the shortening of the larval period, the total life cycle was significantly shorter in offspring from old as compared with those produced within the first month following emergence.

Table 2 lists the duration of each of the first 10 larval stadia for each parental age group. These values are not given beyond the 10th instar because a few of the larvae pupated at the next molt. The table shows that, in addition to the smaller number of molts, the shortening of the larval period associated with an increase in parental age is in part due to a decrease in the time required for most of the larval stadia, the exceptions being the first and tenth.

[1] This experiment was suggested by Professor Th. Dobzhansky, Columbia University. It was supported in part by Grant No. E-2276 from the National Institute of Allergy and Infectious Diseases, Public Health Service.

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Table 1.—Effects of parental age on offspring from an isolated pair of beetles. Values are given with their standard errors.

Age of parents (days)	No. of larvae	Wt. of larvae at 12 weeks (mg.)	Duration of larval period (days)	No. of larval molts	Duration of adult stage (days)	Duration of life cycle (days)
6	27	10.4 ± 2.69	146.1 ± 2.29	13.3 ± 0.15	94.7 ± 6.05	258.3 ± 7.35
20	14	9.7 ± 1.91	141.3 ± 4.00	12.9 ± 0.22	99.8 ± 10.94	257.9 ± 12.17
34	27	32.4 ± 6.91	124.1 ± 2.42	12.0 ± 0.16	101.4 ± 7.42	243.0 ± 7.95
48	35	64.9 ± 7.96	117.9 ± 1.38	11.9 ± 0.10	107.8 ± 8.07	243.3 ± 7.74
63	22	71.0 ± 5.46	108.9 ± 1.54	11.5 ± 0.10	109.2 ± 8.76	235.4 ± 8.01
76	15	67.0 ± 6.65	111.1 ± 1.23	11.8 ± 0.11	95.6 ± 9.78	224.1 ± 10.27

Table 2.—Effects of parental age on the duration of each of the first 10 stadia in offspring from an isolated pair of beetles.

Age of parents (days)	Duration of each stadium (days)										
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	Total
6	3.0	17.1	14.0	12.9	11.0	11.4	10.9	9.4	9.2	9.9	108.8
20	3.5	19.7	13.7	14.0	10.3	9.8	9.1	8.2	8.1	9.0	105.4
34	3.6	16.0	13.1	13.3	9.0	8.6	8.4	8.5	8.2	9.2	97.9
48	3.4	13.9	11.4	11.0	8.5	8.5	8.3	7.8	8.7	9.4	90.0
62	3.7	11.9	11.6	12.9	7.6	7.4	7.6	7.5	8.8	9.9	88.9
76	4.1	13.9	13.1	10.9	7.1	7.3	7.3	7.6	8.0	9.4	88.7

This experiment shows that the increase in rate of growth and the decreases in the duration of the larval stage and in the number of larval molts, associated with an increase in parental age, described by Tracey (1958) and by Ludwig and Fiore (1960), were not caused by selection since they appeared in offspring from each of the four isolated pairs of beetles used in this study. The differences reported here are much more pronounced than those obtained with offspring from mass cultures. In the previous work, with larvae reared under conditions comparable to those used here, offspring from 6-day parents required 134.8 days for the larval period and had 13.5 molts, whereas in those from 63-day parents these values were 121.2 and 12.8. In the present work, the corresponding values for the duration of the larval period were 146.1 and 108.9 days, and for the number of larval molts, 13.3 and 11.5, respectively (table 1). The shortening of adult life associated with an increase in parental age obtained in the previous work did not appear in experiments with offspring from isolated pairs.

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Distinguishing Sexes in Nymphs of the Tomato Psyllid, *Paratrioza cockerelli*[1]

R. DUNCAN CARTER[2]

Means of distinguishing sexes in immature insects are useful in the laboratory where sexes must be treated separately or mating of adults is to be controlled, and in the field where a knowledge of sex ratio is important. The yellowish coloration of the developing testes is sufficiently intense in fourth- and fifth-instar nymphs of the tomato psyllid, *Paratrioza cockerelli* (Sulc), to permit in vivo segregation of the sexes under the dissecting microscope.

Examination of cleared, whole-mounted nymphs reveals that all bear internally a yellowish-orange, roughly U-shaped body, lying almost entirely in the basal half of the abdomen (fig. 1A). This is the mycetome, as illustrated by Rowe and Knowlton (1935). In male nymphs the spindle-shaped testes extend caudad along and beyond the mycetome lobes, forming with the mycetome the H-like marking shown by Essig (1917) and described by Hartman (1937) as characterizing the tomato psyllid nymph (fig. 1B). In the female nymphs a pair of hyaline bodies may be seen posterior to the mycetome (fig. 1A). These apparently are developing ovaries, such as Brittain (1923) has shown to occur in *Psylla mali* Schmidberger.

In third-instar and younger tomato psyllid nymphs, the testis is often so weakly colored as to be almost invisible. In older nymphs, weak coloration of the testes is the exception. Among more than 200 live, fourth- and fifth-instar nymphs examined under the dissecting microscope, the presence of testes was questionable for only 5% of the individuals. Nymphs for which the presence or absence of testes appeared certain were re-examined as adults and found to have been sexed correctly.[3]

Occasionally the mycetome lobes of female nymphs part prematurely (fig. 1C). These nymphs will not be mistaken for males, even in rare instances when the parted lobes appear spindle-shaped and a vestige of the central mass of the mycetome remains. The different coloration and location of the mycetome prevents its being confused with the testes.

Male nymphs of *Paratrioza maculipennis* (Crawford) and *P. lavaterae* (Van Duzee) also have an H-marking cast on the abdomen by the testes and mycetome. Formation of this mark is dependent on a linear arrangement

[1] From a doctoral dissertation, University of California at Berkeley. Accepted for publication November 14, 1960.

[2] Present address: 850 Thornton Street, San Leandro, California. The advice of Professor D. D. Jensen is gratefully acknowledged.

[3] The testes are seen with difficulty through the body wall of the adult male psyllid. In adults, sexes are distinguished by prominent features of the external genitalia, as was shown by Essig (1917).

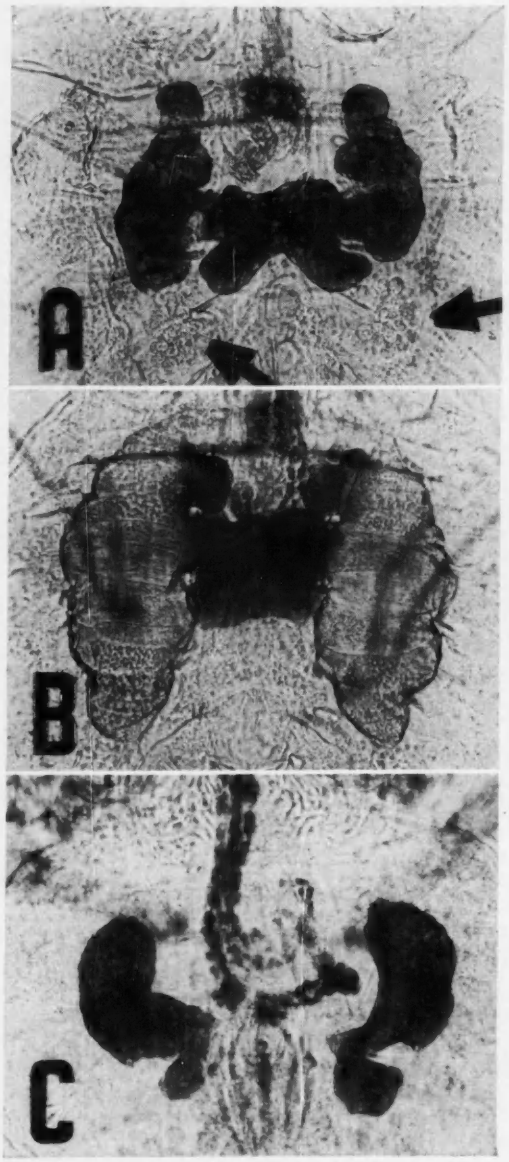

FIG. 1.—Anterior abdominal area of cleared, whole-mounted tomato psyllid nymphs. x77. (A) Female, showing U-shaped mycetome and (arrows) developing ovaries. (B) Male, showing mycetome and testes. (C) Female, lobes of mycetome separated. (From photomicrographs by Victor Duran).

of the testis tubules, a pattern which is but one of many found in the Psyllidae. The testis of *P. cockerelli* consists of two opposed tubules which have a common longitudinal axis. A germanium is situated at each pole of the testis axis, and the tubules are joined in a central transformation zone. A single duct leads mesad from the transformation zone.

According to Brittain (1923) and Witlaczil (1885), the testis of other psyllid species may be V- or Y-shaped. Transformation zones and efferent ducts of the tubules are commonly separate. Lacking the linear testis projecting caudad beyond the mycetome, nymphs of these psyllids do not have an H-marking cast upon the abdomen.

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Characters for Separating Larvae of *Sitona lineata* (L.) and *Sitona hispidula* (Coleoptera: Curculionidae)[1]

HUBERT W. PRESCOTT AND W. H. ANDERSON

Entomology Research Division, Agric. Res. Service, U.S.D.A.

The pea leaf weevil (*Sitona lineata* (L.)), a European pest of legumes, was found by W. Downes (1938) in British Columbia in 1936 where it appears to have been introduced by accident. It has gradually moved southward to legume-producing areas of western Washington and Oregon. In this region its populations have become mixed with those of the clover root curculio (*Sitona hispidula* (F.)) and thus a need was created for data that would be of aid to field workers in separating the two species. The adults of both species have been adequately described by Jackson (1920). Differences such as the comparatively slender body of *lineata*, its recumbent elytral bristles, and its quick, excitable movements contrast with the robust appearance, semi-erect elytral bristles, and slower movementss of *hispidula* so that separation in the adult stage offers no serious problem. The larval stages of both species feed underground upon the root systems of the plants they infest. *S. hispidula* consumes the small lateral feeder roots of clovers and alfalfa, and most economic damage is produced by this species in its larval stage. The larvae of *lineata* feed almost exclusively upon the nitrogen-producing root nodules of their host plants (chiefly peas and vetches) often completely destroying the nodules. This damage is difficult to assess in economic terms but is undoubtedly great. Since the larvae of both species are very similar, it is often difficult to ascertain whether one or both are infesting legume crops under observation. The necessity for data by which the larval stages of *lineata* and *hispidula* could be separated led to the present investigations.

Larvae of several species of the genus *Sitona* have been characterized very adequately by van Emden (1952). Since that paper may not be readily available, the essential characters for recognition of the genus are given below, as are the means of separating larvae of the two species:

Larvae, as stated above, feeding at or in underground parts of plants. Head free, lightly pigmented, with frontal sutures distinct, and with less heavily pigmented, longi-

[1] Accepted for publication November 28, 1960.

FIG. 1

FIG. 3

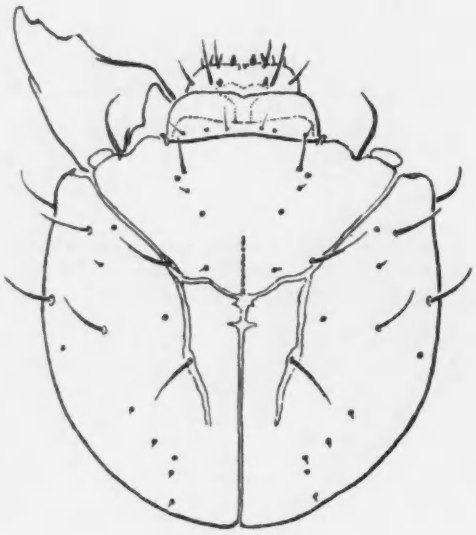

FIG. 2

FIG. 4

FIG. 1.—Epipharynx of *S. hispidula*. FIG. 2.—Head of *S. hispidula*, dorsal view. FIG. 3.—Epipharynx of *S. lineata*. FIG. 4.—Head of *S. lineata*, dorsal view.

tudinal stripes dorsally on epicranium, behind frons. [A glossary of the terms used here is included in a paper by Anderson (1947).] Endocarina present. Frons with four pairs of setae. Accessory sensory appendage of antenna distinctly wider than long. Two setae on anterior margin of labrum spinelike, much stouter than the others on labrum. Postdorsum of meso- and metathorax with four setae of which 1, 3 and 4 are elongate, subequal, 2 short. Postdorsum of typical abdominal segments with five setae of which 1, 3 and 5 are elongate, subequal, 2 and 4 short. All spiracles bicameral, the air tubes shorter than diameter of subcircular peritreme.

Further studies may show that larvae of other species possess the same characters as the two described herein. Thus, such characters may not prove to be sufficient to separate them from all others of the genus. However, we are concerned only with the two species of *Sitona* known to occur as pests in the legume-producing areas of Washington and Oregon. Mature larvae of these species can be separated by very distinct structural characters, which are illustrated in accompanying figures and referred to in the following couplet:

Mandible (fig. 2) with small, accessory tooth near middle of inner margin; epipharynx (fig. 1) with three anterolateral setae; head capsule evidently larger, less obviously circular in dorsal view ..... **S. hispidula**

Mandible (fig. 4) without small tooth near middle of inner margin; epipharynx (fig. 3) with two anterolateral setae; head capsule smaller, rather obviously subcircular in dorsal view ..... **S. lineata**

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